JOURNAL OF AGRICULTURAL RESEARCH

VOL. 47 WASHINGTON, D.C., SEPTEMBER 1, 1933 NO. 5

THE FLIGHT RANGE OF THE HONEYBEE[1]

By JOHN E. ECKERT[2]

Formerly *associate apiculturist, Bureau of Entomology, United States Department of Agriculture*

INTRODUCTION AND REVIEW OF LITERATURE

The economic value of the honeybee depends, for the most part, upon its ability to pollinate flowers and to produce a surplus of honey and beeswax. In selecting a proper location for an apiary, therefore, one must consider not only the flora, climate, topography, and the nature of the soil, but also the distances bees must fly in quest of food. With respect to the last factor, a review of the available literature has failed to reveal much pertinent information.

As early as 1844 Huish (*5, p. 419–429*)[3] reviewed the writings of Huber and others and gave an account of his own experiences in contrast to the opinions then current concerning the distances bees fly in search of nectar and pollen. He stated that some of his bees flew 3 miles to hills richly covered with heath and that he knew of an instance in which bees flew at least 4 miles over water to gather nectar on an island. Other investigators of that period were of varying opinions on this question, giving distances of from 1 to 4 miles, according to Huish. It is apparent from his writings, however, that the distances given were merely estimated and thus subject to considerable error.

Waite (*11*) in 1898 advised that it was necessary to have sufficient bees at least within 2 or 3 miles of an orchard to effect the proper pollination of pomaceous fruits. Hutson (*7*) found under New Jersey conditions that for best results colonies should be scattered within an orchard at the rate of approximately one colony to the acre.

Miller (*8, p. 148*), in Illinois, considered that if the distance was greater than 2 miles the quantity of honey would be reduced. Hutchinson (*6*), in Michigan, thought that bees would range for 2.5 miles in all directions from a given apiary, while Dadant (*3, p. 65*) wrote that as a general rule bees (near Hamilton, Ill.) made their harvest of honey

[1] Received for publication Feb. 4, 1933; issued September 1933. This paper was presented, in part, as a dissertation in partial fulfillment of the requirements for the degree of doctor of philosophy, received in June 1931 from the Ohio State University. The experimental work upon which this paper is based was done while the writer was associate apiculturist, Division of Bee Culture, Bureau of Entomology, U.S. Department of Agriculture, and located at the intermountain bee culture field laboratory at Laramie, Wyo. The experiments were conducted in Wyoming and Colorado under a cooperative agreement with the University of Wyoming.

[2] The writer is indebted particularly to H. Rauchfuss, A. D. Hardy, E. O. Rauchfuss, F. G. Rauchfuss, and G. H. Sechrist for their cooperation, and to Aven Nelson, professor of botany and president emeritus at the University of Wyoming, for the identification of the plants collected in the areas in which the experiments were conducted.

[3] Reference is made by number (italic) to Literature Cited, p. 285.

within a radius of 2 km (1.25 miles). Dadant also stated that he believed bees would fly much farther in following a small valley, or when working on flowers along a road, than in passing above a forest or a hill. Buttel-Reepen (*2, p. 162*) found that bees would orient themselves within a circle of 3 to 4 km (1.86 to 2.48 miles), and where nectar was available at a greater distance from the apiary, with no other source intervening, they would fly 5, 6, and even 7 km (3.11 to 4.35 miles), and under exceptional conditions 12 km (7.46 miles).

One of the most concrete reports reviewed by the writer on the flight range of the honeybee was that of Gowland (*9, p. 54*). Gowland found that the seed yield of fields of sweetclover located beside an apiary was much heavier than that of any other field except one three eighths of a mile away. A field 4.5 miles from the apiary had a very light yield of seed. In the same report he states: "* * * the bees seemed to concentrate their efforts on certain fields rather than to take the fields in order according to distance from their hive." Gowland thought that this might be one reason why the yield of seed did not decrease directly with an increase in distance.

A considerable difference is also found in laws intended to regulate the location of apiaries. A New Zealand law (*1*), for example, requires that beekeepers keep their colonies at least 5 miles from the fruit-drying centers, while a Utah law (*4*) makes it unlawful for migratory beekeepers to locate their apiaries within 2 miles of an established apiary. The same Utah law also requires that all hospital yards (for the treatment of diseased colonies) be located at least 2 miles from other apiaries.

It is reasonable to suppose that the differences in opinion as to the effective flight range of the honeybees may be due to a certain extent to the effect of the locations on the distances the bees had to fly, or they may have been due to a lack of careful observation or to a combination of the two factors. The experiences of such able beekeepers as Miller, Dadant, Hutchinson, and many others have led them to believe that the flight range of the honeybee varies somewhat according to the physical factors of different locations.

The present paper reports the results of experiments conducted in Wyoming and Colorado on the flight range of honeybees and their distribution within a nectar-producing area. The experiments were conducted during the summers of 1927, 1928, 1929, and 1930 and may be divided into three phases. The first observations were made on the flight of bees from colonies located on a prairie during a dearth of nectar when an artificial source of food was provided. In the second series observations were made on colonies located on a stretch of badlands lying between two irrigated districts supporting good growths of alfalfa and sweetclover, and in the third, experiments were conducted with apiaries located within sweetclover territory.

FLIGHT OF HONEYBEES TO AN ARTIFICIAL SOURCE OF FOOD

The first attempt to determine the flight range of the honeybee was made on a wide stretch of prairie west of Laramie, Wyo. The location seemed an excellent one in which to determine the distances bees would fly to an artificial source of food when no important natural source was available.

The Big Hollow, essentially a wind-blown formation about 9 miles long by 3 miles wide and so called because its floor lies between 100 and 150 feet below the level of the surrounding country, contains several fresh-water and alkaline lakes and several ridges (fig. 1). The floor of the formation, which is fairly level to rolling with the exception of the ridges, is covered with grasses, small clumps of cacti, and other vegetation kept short by a lack of moisture and is devoted largely to the grazing of range animals. At the time of the experiment there were no trees or even sagebrush to break the landscape. Only five widely scattered, abandoned homesteads were located in the hollow, and but a small portion of the entire area was under fence.

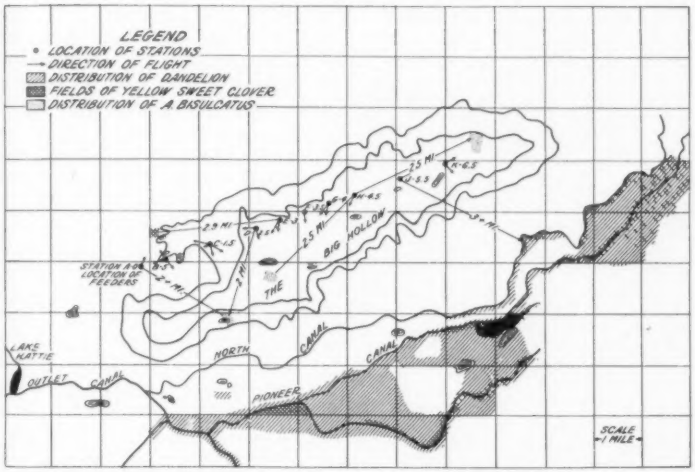


FIGURE 1.—The Big Hollow, west of Laramie, Wyo., where the first attempts were made to determine the flight range of the honeybee.

Numerous wild flowers were present during the period of the experiment, but they were of little importance except for furnishing pollen. Certain members of the genus *Astragalus* which covered small areas in the vicinity of the lakes were visited by the bees for pollen and possibly a little nectar. Near the west end of The Big Hollow 3 acres had been planted to yellow sweetclover several years before, but at the time of the experiment the sweetclover covered only about three fourths of an acre. This field came into bloom near the close of the observations. Other than this one field of sweetclover, the nearest nectar-producing plants, dandelion and sweetclover, were at least 3 miles from the center of The Big Hollow.

EQUIPMENT AND METHODS

On June 1, 1927, twenty 1-story colonies of Italian bees of approximately equal strength were moved into The Big Hollow and distributed at 10 stations which extended in a straight line for 6.5 miles (fig. 1). In the western portion of The Big Hollow the first station, A-0, was located. From this point the line of the stations extended

northeasterly away from the direction of the prevailing winds with the colonies faced toward station A-0. A small shack and a few outbuildings at station A-0 were used as temporary headquarters.

Two feeders (fig. 2) were placed in the open at station A-0 and were kept filled with a sirup made of 20 pounds of granulated sugar and 5 pounds of sweetclover honey dissolved in 75 pounds of water. This solution was colored light red with a vegetable dye found to be noninjurious and nonrepellent to the honeybee.

In order to determine from what stations the bees came or to what stations they returned after their visits to the feeders, the majority of bees in one colony at each station and most of the bees that came to the feeders were marked with distinctive colors. The various colors were applied to the bees at the stations in the form of a fine spray as they crawled up the sides of a box into which they had been shaken. The coloring materials consisted of suspensions of paint pigments in shellac and ethyl alcohol, 1 part shellac and 1 part pigment, by weight, to 4 parts of alcohol. Thus the bees in one colony at station B-0.5 [4] were marked with burnt umber, those at station C-1.5 with Indian red, etc. Most of the bees that visited the feeders were marked individually with vermilion.

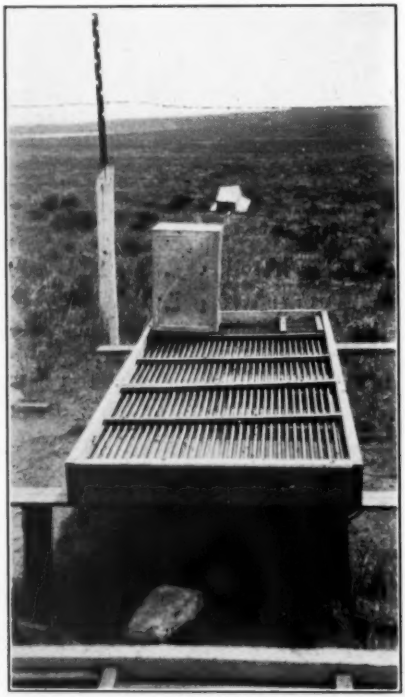


FIGURE 2.—Type of feeder for honeybees used in The Big Hollow.

Although spraying the bees with the alcohol-shellac mixture apparently had no lasting harmful effect upon them, it did not prove a success, as but small quantities of the pigments adhered to their bodies. Some of the bees were well marked, but they were too few to be of much use in determining the flight from any one station or in finding the marked bees in the field. Several hundred bees in each colony were later marked individually, and the pigments adhered to them for many days.

In order to determine whether the bees had procured an appreciable quantity of sirup or any other food, whenever the weather conditions permitted each colony was weighed before flight started in the morning and again after flight had stopped for the day.

Records were kept of the general climatic conditions during the period of the experiment.

[4] The numbers after the station letters refer to the distance in miles each station was located from the feeders.

At each station pollen was collected from returning bees at various intervals for later determination.

In many instances when bees were discovered on plants in the field, they were marked in order that they could be identified later at their hives. When bees so marked in the field were found in their hives, the distance between the hive and the area in which they were marked was recorded.

The hives at each station were searched, generally near the close of each day, for bees marked in the field or at the feeders to determine if any sirup was being carried.

RESULTS

The bees at station A-0 flew to the feeders within a few hours after they had been set out and obtained a significant quantity of sirup during the period of the experiment. The bees at station B-0.5 were at the feeders on the second day after the sirup had been made available. The colonies at that station, however, did not accumulate enough sirup during the entire time of the experiment to show an increase in weight, although the loss was less than that of colonies at the other stations. The bees of only one colony at station C-1.5 found the feeders and then only after some of the field bees had been carried to the feeders where they were fed, marked, and released. The day after this was done, other bees from the same colony also found the feeders. The colonies at station C-1.5 lost weight during the period of the experiment, but the average loss in weight was less than that recorded at the more distant stations (table 1). No bees located beyond the 1.5-mile station were ever seen at the feeders.

TABLE 1.—*The average net gain or loss in weight, by stations, of the colonies in The Big Hollow, June 5 to July 10, 1927, when sugar sirup was used as a source of food*

Station	Gain (+) or loss (−) in weight	Station	Gain (+) or loss (−) in weight
	Kilograms		*Kilograms*
A-0	+2.33	F-3.5	(a)
B-0.5	−1.48	G-4	−5.27
C-1.5	−3.40	H-4.5	−5.48
D-2.5	−5.49	J-5.5	−4.04
E-3	−5.48	K-6.5	−3.51

[a] Queenless.

Several attempts were made to induce the bees to fly farther than 1.5 miles by baiting them with sirup-filled tins which were moved by short stages in the direction of the feeders. No bees could be made to follow these tins for more than 0.7 mile. This may have been due to the general absence of landmarks, as in one instance it was noted that a marked bee, bearing pollen, made a mistake of one-half mile in the location of its own hive. An automobile used in making the rounds to the stations had stopped at the station from which the marked bee came before moving on to the next station, one-half mile distant. The bee evidently included the automobile among the landmarks when it left for the field and in returning flew to the station at which the automobile had stopped.

Bees were traced for at least 3 miles from several stations and were found carrying certain pollens that were available only outside of The Big Hollow.

Near the close of the experiment the field of yellow sweetclover near station A-0 came into bloom, as did also the sweetclover growing to the east and south of the line of colonies. The bees deserted the feeders for these fields and carried sweetclover pollen to all stations but F-3.5. The two colonies at this station were queenless during the greater part of the experiment. Several hundred bees were marked as they worked in the sweetclover near station A-0. Bees thus marked were found at stations A-0, B-0.5, C-1.5, D-2.5, and E-3, but at none of the other stations. The bees at the stations beyond E-3, with the exception of F-3.5, had to fly out of The Big Hollow, a distance of at least 3 miles, for the sweetclover pollen they obtained.

TABLE 2.—*Weather conditions at station A-0 in The Big Hollow in 1927*

Date	Wind				Temperature			Character of sky
	Average velocity	Prevailing direction	Maximum velocity	Direction of maximum velocity	Highest	Lowest	Average	
	Miles per hour		*Miles per hour*		*° F.*	*° F.*	*° F.*	
June 4	8.8	NE.	16.0	N.	80	61	71.1	Partly cloudy.
June 5	11.7	NW.	17.5	W.	57	47	58.9	Do.
June 6	3.0	NW.	13.0	NE.	67	47	59.9	Do.
June 7	10.1	NW.	21.5	N.	79	48	68.5	Do.
June 8	17.6	SW.	30.5	SW.	81	53	72.7	Do.
June 9	16.5	W.	28.5	NW.	72	58	67.7	Clear.
June 10	13.6	SW.	22.5	S.	82	48	69.9	Partly cloudy.
June 11 [a]	9.5	SW.	23.5	SE.	74	50	63.7	Do.
June 12	13.0	SE.	19.0	E.	52	43	48.2	Do.
June 13	11.0	SE.	13.8	SE.	59	41	50.2	Do.
June 14	5.4	SE.	14.0	NE.	68	42	55.1	Cloudy.
June 15 [b]	16.0	N.	28.0	N.	53	48	49.4	Do.
June 16	11.4	NW.	24.5	NW.	68	37	59.0	Partly cloudy.
June 17	17.9	W.	34.5	W.	74	49	61.2	Do.
June 18	10.7	S.	23.5	NW.	77	55	66.3	Do.
June 19	8.0	SW.	35.5	W.	76	50	61.3	Do.
June 20	20.2	N.	26.5	N.	65	54	61.5	Clear.
June 21	16.7	N.	26.0	N.	62	49	55.5	Partly cloudy.
June 22	2.7	(?)	16.0	S.	70	40	61.8	Clear.
June 23	22.7	W.	32.5	SW.	84	66	78.9	Do.
June 24	21.7	W.	32.5	W.	87	69	80.5	Do.
June 25	18.1	SE.	30.5	SE.	84	55	72.2	Do.
June 26	19.3	SW.	30.5	SW.	86	68	79.8	Partly cloudy.
June 27	15.3	SW.	24.5	SW.	79	63	70.2	Do.
June 28	6.6	SE.	13.0	NW.	66	58	60.5	Do.
June 29	13.6	SW.	41.0	SW.	74	55	63.6	Do.
June 30	18.2	NW.	28.5	W.	65	49	58.5	Do.
July 1	10.6	SW.	23.5	W.	75	47	65.9	Clear.
July 2	11.7	SW.	28.0	SW.	80	54	72.3	Do.
July 3	15.8	SW.	27.0	SW.	80	60	72.4	Partly cloudy.
July 4	16.8	SW.	37.0	W.	81	59	67.3	Do.

[a] Last observations taken at 5:30 pm.
[b] No observations made between 8 a.m. and 12:30 p.m.

The combs in the colonies at stations G-4, H-4.5, J-5.5, and K-6.5 showed that the bees obtained nectar and pollen apparently from the dandelion which grew abundantly at distances of 3 and 4 miles from these stations. The colonies at stations J-5.5 and K-6.5 obtained enough nectar from dandelion and sweetclover to minimize losses in weight.

The weather conditions (table 2) that prevailed during the period of the experiment were not altogether favorable to bee flight. The

comparatively low temperatures, together with the large number of cloudy and windy days, tended to retard the activities of the bees. It was evident, however, that the bees flew farther for pollen and nectar than they did for sirup. Whether or not bees will fly more than 1.5 miles to an artificial source of food in locations containing more landmarks was not ascertained.

FLIGHT OF HONEYBEES TO A NATURAL SOURCE OF FOOD

LOCATION

The second phase of these experiments was conducted in northwestern Wyoming in the summers of 1927, 1928, and 1929, on two irrigated areas separated by at least 17 miles of badlands (fig. 3).

The general contour of the country between the two irrigated areas is comparatively level for the first 5 miles from its northern border and then becomes rolling to rough until the bench land at the south is reached. Drainage is toward the Shoshone River on the north, and the slope of the land is such that parts of the green fields and the trees bordering the river are visible from the badlands at a distance of several miles. In fact, both irrigated areas can be seen from many points along the old winding stagecoach road that connects the two.

The creeks in the badlands (fig. 3) were dry during the summer months except for short periods after rains and were marked by wide flood plains overgrown with denser vegetation than that which grew on the higher land.

The summer vegetation in this area consisted, for the most part, of small clumps of cacti (*Opuntia fragilis*), stunted sagebrush (*Artemisia tridentata*), some greasewood (*Sarcobatus* sp.), an admixture of the saltbushes (*Atriplex*), rabbitbrush (*Chrysothamnus*), which grew along the stream beds, and a scattering of various grasses, sedges, and dead stalks of spring-flowering plants. The small composite *Machaeranthera tanacetifolia* grew in abundance on the badlands in 1927 and 1928, and its color added a dash of blue to the otherwise gray aspect (fig. 4). Only a few gnarled and twisted cottonwoods were found along the banks of Coon and Whistle Creeks. The only plants from which bees could secure nectar were confined to the irrigated areas. Numerous prairie-dog mounds and large ant hills, the latter in the center of cleared spaces several feet in diameter, and a double row of telephone poles which crossed the badlands between the irrigated areas may have served as landmarks for the bees in their flights over this semidesert land. The irrigated areas, on the other hand, were known to be good beekeeping territory, and a number of commercial apiaries were located there.

EQUIPMENT AND METHODS

As it was evident that the badlands could provide no appreciable source of nectar for bees during the period of the experiments, the general plan of procedure called for the placing of colonies on the badlands at various distances from the irrigated area bordering the Shoshone River. The bees would thus be compelled to fly to the irrigated areas for nectar, and it was thought that records of the gains or losses in weight of the colonies would indicate the effect of distance upon their activities in the matter of honey production. The

fact that they actually flew to the irrigated areas was checked further by the identification of the pollens they carried.

The colonies used in the experiments in 1927 and 1928 were taken from apiaries located near Powell, Wyo., and as far as possible were of uniform strength in adult bees and brood. Each colony used in 1929 consisted of 4 pounds of bees and 4 frames of brood taken from

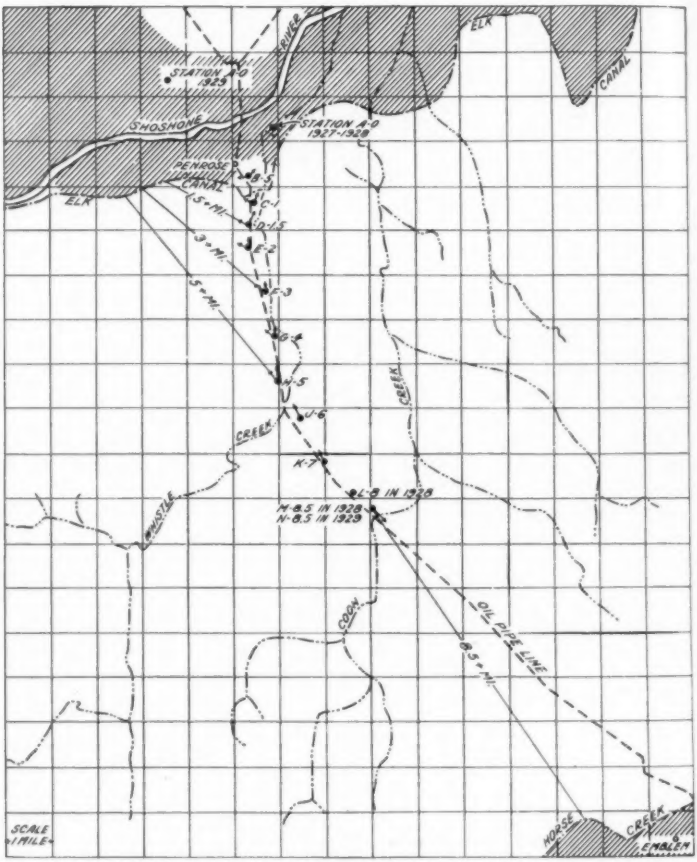


FIGURE 3.—A diagram of the district east of Powell, Wyo., in which the honeybee-flight experiments were conducted in 1927, 1928, and 1929. The shaded areas represent the irrigated areas in which fields of alfalfa and sweetclover were located. The badlands lie between them. Colonies were located at the stations numbered and the directions of flight are indicated by arrows.

overwintered colonies. An attempt was made to secure the 4 pounds of bees and a queen from 1 colony for each colony formed. In several instances, however, bees had to be obtained from two or more colonies in order to secure the 4 pounds. In such cases laying queens were introduced into the newly formed colonies. Equal numbers of Caucasian and Italian colonies were included in each of the 3 years. The

colonies used in 1927 and 1928 were somewhat stronger than those used in 1929.

The colonies were placed in practically the same locations each year, although certain changes in the number of stations were made during 1929, as will be described later.

The stations, each consisting of several colonies, were located with the aid of a map issued by the United States Reclamation Service (*10*). The distances between the stations and certain points in the irrigated area bordering the Shoshone River were checked either by an automobile odometer or by surveying instruments. Consequently the distances given in this report represent the minimum distances the bees had to fly on quiet days. On windy days these distances would be increased somewhat, especially for the bees located at the stations beyond 5 miles, as on such days the bees flew close to the ground and often had to deviate from a straight line.

In 1927 three colonies were placed at each of the first 10 stations (fig. 3). The first group of colonies, at station A-0, was 0.5 mile

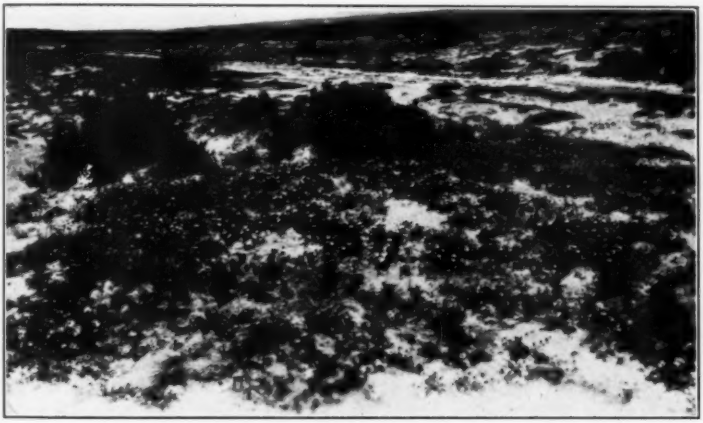


FIGURE 4.—A typical spot on the badlands, showing the characteristic vegetation.

within the irrigated area. The other 9 stations were on the badlands in a line extending practically at right angles to the irrigated area along the Shoshone River, the last station (K-7) being 7 miles from a source of nectar.

In 1928, 5 colonies were placed at each of the first 2 stations, 4 at station C-1, and 3 at each of the other 7 stations. After the first week one colony was moved from station B-0.5 and another from C-1 to the positions indicated as L-8 and M-8.5, respectively.

Forty-two colonies were used in 1929. Station A-0 was placed farther within the irrigated area in what was considered an even better location than it occupied in 1927 and 1928; it contained 4 colonies, 2 Caucasian and 2 Italian. The next 9 stations, which occupied the same positions as during the 2 previous years, also contained 2 Italian and 2 Caucasian colonies each. The eleventh station, N-8.5, contained 1 Caucasian and 1 Italian colony. After observations had been made for 13 days, the colonies at stations K-7, J-6, H-5, and G-4

were moved to stations closer to the source of nectar. A second shift of colonies was made after another 13-day period, at which time the colonies at stations C-1, E-2, and F-3 were concentrated at stations A-0, B-0.5, and D-1.5.

None of the colonies were manipulated more than was necessary to provide supers or stores as needed, and all were examined alike on the same days. Colonies more than 4 miles from the irrigated areas were supplied with honey. There was no swarming during the 3 years, although some colonies became queenless. The records of the queenless colonies have not been included in the data.

All hives at the first 10 stations were weighed each evening after the bees had stopped flying, unless weather and road conditions prohibited. When the observations were omitted on any day during the period of the experiment, the figure recorded for the following day represented the net loss or gain for 2 days, so that this figure will be larger than when only 1 day's loss or gain is included. Generally, there was less than an hour's difference between the time the first and the last colony was weighed. In 1928 it was impracticable to weigh the colonies at stations J-6 and K-7 as often as the other colonies because of rains which made Whistle Creek impassable. The colonies at these two stations and those at stations L-8 and M-8.5 were moved across this creek before the termination of the experiment.

OBSERVATIONS AS TO DISTANCE OF FLIGHT

The bees began to carry in pollen within a few hours after they were placed at the stations. The fact that the pollen carried was sweet clover indicated that the bees flew from 0.5 mile to 7 miles in 1927 and at least 8.5 miles in 1928 and 1929. As these figures represent the minimum distances from the nectar source, additional flight was necessary for the bees to obtain a load of pollen or nectar. In all probability the bees at the 8.5-mile station flew at least 18 or 20 miles on each round trip.

All bees within 7 miles of the irrigated area bordering the Shoshone River flew north, while those at the 8.5-mile station flew to the irrigated area in the opposite direction. The nectar sources at the south were approximately 0.1 mile closer to the station 8.5 miles out than were the nectar sources at the north. No bees were observed to return to the 8.5-mile station from the north.

The direction of flight of the bees from any one station was generally over a narrow angle and in one particular direction, although some bees flew in other directions as well.

EFFECT OF DISTANCE OF FLIGHT UPON THE GAIN OR LOSS IN WEIGHT OF COLONIES

Experiments in 1927

All the normal colonies at stations within 4 miles of the irrigated area increased in weight. Colonies beyond the 4-mile point lost weight. The average gain in weight of the colonies at station A-0, located within the source of nectar, was somewhat less than that of the colonies 0.5 mile out on the badlands. From the 0.5-mile station the average gain in weight per station decreased gradually with an increase in distance, until a loss was recorded at the station 5 miles out, and the average loss became greater at stations J-6 and K-7, respectively (table 3 and fig. 5).

TABLE 3.—*Daily average net gain (+) or loss (−) in weight of the colonies at the different stations, August 1927*

Station	Colonies	Average gain or loss per colony, in kilograms, on August—																	Total of daily average net gains or losses in weight	Average daily net gain or loss in weight for 18-day period
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	*16	17	18		
	Number																		*Kilograms*	*Kilogram*
A-0	2	−0.25	+0.29	+1.81	+1.34	+1.30	+0.11	+0.12	+1.50	+1.67	−0.37	+2.08	−0.08	+0.17	+0.21	+0.80	+0.77	+0.01	+11.48	+0.637
B-0.5	3	−.14	+.33	+2.40	+1.95	+1.81	+.30	+.17	+1.83	+1.87	−.06	+2.05	−.17	+.48	+.10	+.58	+.95	−.08	+14.37	+.798
C-1	3	−.14	+.16	+1.74	+1.68	+1.36	−.17	+.12	+1.18	+1.55	−.16	+2.05	−.72	+.30	+.06	+.52	+.89	+.15	+10.57	+.587
D-1.5	3	−.34	+.09	+2.00	+1.64	+1.62	+.14	−.12	+1.19	+1.30	−.15	+1.89	−.76	+.22	−.07	+.44	+.67	−.10	+9.66	+.537
E-2	3	−.02	−.14	+.87	+1.64	+1.42	−.17	−.24	+1.08	+1.36	−.24	+1.88	−.84	+.27	+.23	+.36	+.84	−.06	+8.24	+.458
F-3	3	−.10	−.20	−.01	+.168	+2.00	−.82	−.53	+1.24	+1.38	−.31	+1.77	−.92	+.05	+.19	+.30	+.70	−.15	+6.27	+.348
G-4	3	−.18	−.08	−.51	+.31	+1.88	−.54	−.62	+.79	+.91	−.31	+1.20	−.77	−.13	+.02	−.05	+.51	−.07	+2.36	+.131
H-5	3	−.15	−.20	−.48	−.43	+.71	−.47	−.49	+.24	+.52	−.32	+.78	−.74	−.12	−.06	−.18	+.18	−.18	−1.39	−.077
J-6	3	−.18	−.14	−.37	−.49	−.20	−.24	−.35	−.09	+.24	−.34	+.56	−.75	−.08	−.02	−.24	.0	−.14	−2.83	−.157
K-7	3	−.04	−.04	−.24	−.45	−.43	−.40	−.26	−.19	−.20	−.28	−.30	−.57	+.07	+.02	−.10	−.30	−.20	−3.91	−.217

* No records were obtained for Aug. 15, but those obtained on Aug. 16 include the net loss or gain for both Aug. 15 and 16.

Colonies at all stations lost weight on the first day after they had been placed in position. On the second day the colonies at the stations up to and including station D-1.5 gained weight. A gain was made at the 2-mile station on the third day. Stations F-3 and G-4 showed the first gain on the fourth day, and station H-5 made a gain on the fifth day. The colonies 6 miles away from the source of nectar made a small gain on the ninth day, but thereafter the total losses were greater than the gains. The colonies at the 7-mile station made a slight gain in weight on the thirteenth day, but as in the case of the colonies at stations H-5 and J-6 the average total losses were greater thereafter than the gains (table 3).

From the standpoint of honey production, 1927 was considered a poor year by the beekeepers operating in the territory where these experiments were conducted.

Experiments in 1928

Inasmuch as the colonies at the 5-, 6-, and 7-mile stations lost weight during 1927, each colony in 1928 was given a shallow super of honey as a reserve food chamber, but these had to be removed within a few days and replaced with supers of foundation in order to provide room for the nectar that the bees were bringing in. The food chambers were left on the colonies at stations L-8 and M-8.5.

The colonies at each of the first 10 stations made material gains. The average daily gain or loss in weight per colony was again less at the station within the nectar-producing area than at some of the stations out on the badlands. The effect of distance was less pronounced in 1928 than it was in 1927. In 1928 a distance of 3 to 5 miles showed little effect on the average daily gain or loss in weight, although the average gain was greater for the colonies at C-1, D-1.5, E-2, and F-3 than for those at the other stations. The average data for this period show that the colonies 0.5 to 2 miles away from the irrigated area made greater gains than the colonies within the area. Beyond the 3-mile point a gradual decrease in weight roughly proportional to the increase in distance was recorded. The average daily gain, however, of the colonies 7 miles from the source of nectar in 1928 closely approximated that of the colonies within the irrigated area in 1927 (fig. 3 and tables 3 and 4).

TABLE 4.—*Daily average net gain (+) or loss (−) in weight of the colonies at the different stations, July 1928*

Station	Colonies	Average gain or loss per colony, in kilograms, on July—															Total of daily average net gains or losses in weight	Average daily net gain or loss in weight for 23-day period
		3	5	8	10	12	14	15	17	19	20	21	22	23	24	25		
	Number																*Kilograms*	*Kilograms*
A-0	5	+0.30	+1.14	+0.87	+1.06	+2.39	+2.32	+0.82	+1.15	+3.49	+0.48	+1.80	+1.96	+1.63	+1.95	+1.33	+22.69	+0.987
B-0.5	4	+.38	+1.11	+.90	+.68	+2.53	+2.81	+.59	+1.25	+3.82	+.66	+2.05	+1.80	+1.69	+1.67	+1.06	+23.00	+1.000
C-1	3	−.07	+1.13	+1.16	+1.09	+2.89	+4.25	+1.38	+1.85	+4.89	+.94	+3.09	+2.40	+2.55	+3.05	+2.48	+33.08	+1.438
D-1.5	3	−.78	+.84	+1.02	+1.07	+2.50	+3.48	+1.08	+1.63	+3.17	+.81	+2.40	+2.27	+2.09	+2.11	+1.14	+24.83	+1.080
E-2	3	−.48	+.43	+.74	+.80	+3.07	+3.53	+1.16	+1.57	+3.16	+1.04	+2.78	+2.32	+2.19	+2.50	+1.23	+26.04	+1.132
F-3	3	0.00	+.45	+2.36	+1.40	+3.81	+3.15	+.93	+1.33	+2.80	+.77	+2.09	+1.61	+1.44	+1.90	+1.02	+25.06	+1.090
G-4	3	−.03	+.53	+1.02	+.94	+1.91	+1.88	+.69	+1.46	+1.13	+.63	+1.86	+1.42	+1.43	+1.87	+.77	+17.51	+.761
H-5	3	−.15	+.75	+1.31	+1.19	+2.89	+2.75	+1.19	+1.55	+1.16	+1.13	+2.15	+1.45	+1.87	+1.91	+1.06	+22.21	+.966
J-6 [a]	3	+.02	+1.01	.....	+.64	.....	.....	.....	+8.45	.....	.....	.....	.....	+3.83	.....	.....	+13.95	+.664
K-7 [a]	3	−.33	+.79	.....	+1.60	.....	.....	.....	+6.74	.....	.....	.....	.....	+3.47	.....	.....	+12.27	+.584

The colonies at stations J-6 and K-7 were weighed at irregular intervals, the last weights being taken on July 23. The average was therefore for a 21-day period.

The colonies at stations A-0 and B-0.5 made an average gain in weight the first day, while all the other colonies lost weight, with the exception of those at F-3, which showed no change, and at J-6, where there was a slight gain. The colonies were not weighed again until the third day, by which time all had increased in weight (table 4).

Beekeepers in the vicinity considered honey production to be above the average in 1928.

Experiments in 1929

First period

During the first part of the experiment in 1929 (July 3 to 15) the colonies were in practically the same positions as in 1927 and 1928, except that station A-0 was moved to what was thought to be a more favorable location within the irrigated area, and only one station, N-8.5, was situated beyond K-7.

The colonies on the badlands at stations B-0.5, C-1, D-1.5, and E-2 again made greater average gains in weight than the colonies at station A-0, which was within the irrigated area. Beyond the 2-mile point the adverse effect of distance was increasingly apparent, until losses were recorded at stations J-6 and K-7, as well as at N-8.5 (table 5).

Table 5.—*Daily average net gain (+) or loss (−) in weight of the colonies at the different stations during the first period, July 3 to 15, 1929*

Station	Colonies	Average gain or loss per colony, in kilograms, on July —									Total of daily average net gains or losses in weight	Average daily net gain or loss in weight for 13-day period
		3	4	6	9	10	11	12	14	15		
	Number										*Kilograms*	*Kilograms*
A-0	[a] 3	+0.85	+1.03	+2.39	+1.41	+1.34	+0.61	+1.86	+1.36	+0.64	+11.49	+0.884
B-0.5	4	+1.14	+1.24	+3.06	+1.73	+1.33	+.64	+1.75	+1.55	+.82	+13.26	+1.020
C-1	4	+1.38	+1.38	+2.86	+2.30	+.90	+.41	+1.54	+1.47	+.37	+12.61	+.970
D-1.5	4	+1.48	+1.55	+3.25	+1.83	+.94	+.21	+1.59	+1.32	+.21	+12.38	+.952
E-2	4	+1.53	+1.56	+3.50	+1.31	+.91	+.26	+1.63	+1.15	+.15	+12.00	+.923
F-3	3	+1.05	+1.17	+3.41	+.93	+.60	−.11	+1.34	+1.13	+.03	+9.55	+.735
G-4	4	+.18	+.43	+1.63	+.44	+.26	−.13	+.78	+.61	−.07	+4.13	+.318
H-5	3	−.13	+.03	+.84	+.08	+.10	−.24	+.45	+.52	−.18	+1.47	+.113
J-6	4	−.18	−.26	−.29	−.43	+.10	−.33	−.02	+.05	−.21	−1.57	−.121
K-7	4	−.03	−.39	−.43	−.26	−.14	−.17	−.27	−.16	−.12	−1.97	−.151
N-8.5	2										−1.75	−.134

[a] 2 of the 5 colonies originally located at station A-0 became queenless during this period and, being abnormal, their production was not recorded.

In this period the colonies were not weighed until the second day after they had been placed on location. By that time all colonies up to and including those at station G-4 gained weight. On the following day the colonies at the 5-mile station gained weight while those at the more distant stations lost weight. On the ninth day the colonies at station J-6 gained weight. (This coincided with the data of colonies located at the same station in 1927.) The colonies at stations K-7 and N-8.5 did not gain weight during any day of this period.

SECOND PERIOD

In order to demonstrate more clearly the effect of length of flight on the change in weight of certain of the colonies moved, on July 16 some of the colonies from stations G-4, H-5, J-6, and K-7 were moved to stations A-0, B-0.5, D-1.5, E-2, and F-3, as indicated in table 6. One colony (no. 20) was moved from station E-2 to station A-0. This increased the number of colonies under observation at points which seemed to be the most important from the standpoint of practical honey production.

TABLE 6.—*Changes made in the location of colonies at the beginning of the second period, July 17 to 29, 1929, and a comparison between the gains (+) or losses (−) in weight of the colonies in their new locations and in their old locations during the first period*

Colony no.	Old location	New location	Distance moved	Average daily net gain or loss in weight	
				At old location	At new location
			Miles	*Kilograms*	*Kilograms*
20	E-2	A-0	4.0	+1.116	+1.460
37	K-7	A-0	9.4	−.154	+1.599
39	K-7	A-0	9.4	−.152	+1.593
27	G-4	B-0.5	3.5	+.462	+1.006
34	J-6	B-0.5	5.5	−.096	+1.412
36	J-6	B-0.5	5.5	−.079	+.940
26	G-4	D-1.5	2.5	+.214	+.892
29	H-5	D-1.5	3.5	+.050	+1.235
40	K-7	D-1.5	6.5	−.147	+1.459
25	G-4	E-2	2.0	+.375	+.672
28	G-4	E-2	2.0	+.220	+.516
33	J-6	E-2	4.0	−.142	+.569
35	J-6	E-2	4.0	−.166	+.619
30	H-5	F-3	2.0	+.065	+.806
31	H-5	F-3	2.0	+.225	+.336
38	K-7	F-3	4.0	−.153	+1.140

During the forenoon of the day after the colonies were moved, several hundred bees were flying around the spot where station J-6 had been located. Caucasian and Italian bees were present in approximately equal numbers, and most of them were carrying sweetclover pollen. As two of the colonies from station J-6 had been moved at least 4 miles to station E-2, it was evident that some of the field bees, on leaving their hives on the following morning, had flown to the irrigated area, obtained pollen, then returned over the old route to which they had been accustomed, and in so doing covered a minimum distance of 8 miles.

A larger number of bees, most of them bearing sweetclover pollen, were found flying around the place where station H-5 had been. Two of the colonies from this station had been moved 2 miles to station F-3, and one had been moved 3.5 miles to station D-1.5. Still more bees were found clustered on sagebrush or flying around the spot where station G-4 had been; most of them were also carrying sweetclover pollen. Two of the colonies from this station had been moved 2 miles, another 2.5 miles, and the fourth colony 3.5 miles. In gathering pollen and in returning to their old locations, these bees had flown a minimum of 4.5 to 6 miles. In all probability some of the bees from all the colonies moved, with the exception of those moved from

station K-7, returned to their former locations, thus flying minimum distances of from 6.5 to 8 miles.

The bees that returned to the old locations were allowed to enter supers and were taken back to the new locations the same evening. On the second day after the colonies had been moved, bees were flying around the old locations at stations J-6, H-5, and G-4, and they were again returned to their hives. On the following day only a few bees were found flying around the old location of G-4. It is well known that field bees sometimes remain out overnight and return to their hives in the morning. The fact that no bees were found flying around the former location of station K-7 indicates that the field bees did not generally stay out the night the colonies were moved.

During the second period the colonies at all the stations collected sweetclover pollen; those at the first six stations made appreciable gains; while those at station N-8.5 lost weight (table 7). A distance of 1 mile evidently did not appreciably reduce the gain of the colonies, but beyond that point the reduction in gain increased with the distance of flight. This apparent effect of distance may have been accentuated by the fact that more of the field bees from the colonies moved to stations E-2 and F-3 may have been lost than was probably true of the colonies moved to the other station.

TABLE 7.—*Daily average net gain (+) or loss (−) in weight of the colonies at the different stations during the second period, July 17 to 29, 1929*

Station	Colonies	Average gain or loss per colony, in kilograms, on July—												Total of daily average gains or losses in weight	Average daily gain or loss in weight for 13-day period
		17	[a] 19	20	21	22	23	24	25	26	27	28	29		
	Number													*Kilograms*	*Kilograms*
A-0	[b] 7	+1.39	+2.11	+0.99	+1.03	+1.67	+1.46	+1.54	+1.51	+0.90	+0.44	+1.62	+1.48	+16.14	+1.241
B-0.5	7	+1.71	+2.39	+1.21	+.84	+2.12	+1.60	+1.55	+1.89	+.71	+.53	+2.37	+2.06	+18.98	+1.460
C-1	4	+1.87	+2.27	+1.22	+.42	+2.11	+1.75	+1.22	+1.84	+.40	+.51	+2.08	+1.79	+17.48	+1.345
D-1.5	7	+1.53	+1.74	+.88	+.23	+1.82	+1.92	+1.15	+1.91	+.11	+.47	+2.36	+1.91	+16.03	+1.233
E-2	7	+.80	+.97	+.58	−.03	+1.19	+1.63	+.76	+1.21	.00	+.12	+1.87	+1.71	+10.81	+.832
F-3	6	+.89	+1.01	+.41	−.11	+1.00	+1.68	+.53	+1.13	−.03	−.15	+1.89	+1.94	+10.19	+.784
N-8.5	2													−1.74	−.134

[a] No records taken on July 18.
[b] One of the colonies at this station which became queenless during the first period was made queen-right, resumed normal activities, and was thereafter included in the record.

88822—33——2

The effect of moving the colonies nearer to the source of nectar, as shown in table 6, was quite striking in some instances. The greatest difference occurred in those colonies that had been moved from 6 and 7 miles from the source of nectar to within the irrigated area or 1.5 miles from it. These colonies had lost weight during the first period of 1929 but gained when placed in the new locations. In every instance colonies moved nearer to the source of nectar made greater gains than they had in their former positions (table 6) and in several instances they showed greater gains than the colonies already located at the stations to which they had been moved (table 9). These gains were made in spite of the loss of field bees due to the change in locations. It was evident that the colonies at the more distant stations lost weight during the previous period because of the distances that separated them from the source of nectar rather than on account of any insufficiency in the number of field bees.

THIRD PERIOD

The colonies at stations C-1, E-2, and F-3 were moved to stations A-0, B-0.5, and D-1.5, respectively, on the evening of July 29, as indicated in table 8. The same procedure was followed as that used during the previous period, although even greater precautions were taken to see that the bees reoriented themselves in the new locations.

TABLE 8.—*Changes made in the locations of colonies at the beginning of the third period, July 31 to Aug. 9, 1929, and a comparison between the gains (+) or losses (−) in weight of the colonies in their new locations and in their old locations during the second period*

Colony no.	Old location	New location	Distance moved	Average daily net gain or loss in weight	
				At old location	At new location
			Miles	*Kilograms*	*Kilograms*
9	C-1	A-0	3.6	+1.436	+1.325
10	C-1	A-0	3.6	+.888	+.820
11	C-1	A-0	3.6	+1.398	+.654
12	C-1	A-0	3.6	+1.658	+1.358
41	N-8.5	A-0	10.75	−.152	+1.824
42	N-8.5	A-0	10.75	−.115	+1.863
17	E-2	B-0.5	1.5	+1.656	+1.547
18	E-2	B-0.5	1.5	+.806	+1.281
19	E-2	B-0.5	1.5	+1.006	+1.386
25	E-2	B-0.5	1.5	+.672	+.883
28	E-2	B-0.5	1.5	+.516	+.749
33	E-2	B-0.5	1.5	+.569	+1.160
35	E-2	B-0.5	1.5	+.619	+.908
21	F-3	D-1.5	1.5	+.692	+.825
22	F-3	D-1.5	1.5	+.626	+.613
23	F-3	D-1.5	1.5	+.705	+.728
24	F-3	D-1.5	1.5	+.735	+1.174
30	F-3	D-1.5	1.5	+.806	+1.064
31	F-3	D-1.5	1.5	+.336	+.512

Soon after noon of the next day, which was bright and clear, many bees had returned to their old location (station F-3), and by evening 3.4 pounds of bees (approximately 14,000 bees) had collected in the hive placed there to trap them. Most of these bees were loaded with sweetclover pollen and nectar. The colonies from this station had been moved 1.5 miles closer to the source of nectar. Only about one

sixth as many bees from station E-2, which was also moved 1.5 miles closer to the source of nectar, returned to their old location as returned to station F-3. Field bees in much reduced numbers continued to return to their old locations on the second day after the colonies had been moved. These were again collected and taken to the new locations. The third day was a poor day for flight, and only a few hundred bees were found flying around the old location of station F-3. As in the former instances, the returned bees were laden with pollen, much of which was from sweetclover, and with nectar.

The fact that so many bees returned to their former locations was, without doubt, due to the similarity of the entire territory and further to the fact that the bees that returned had evidently worked in the same locations within the irrigated area as they had before being moved. It is possible that other bees may have been lost on the badlands.

The average daily gain of the colonies that were not moved showed practically the same relation to distance as during the previous period (table 9). The average gain of the colonies 0.5 mile from the nectar-producing area was again greater than that of the colonies located within it (table 10).

TABLE 9.—*Average daily net gains in weight of colonies originally located at the stations where consolidations were made, during the 3 experimental periods in 1929*

Station	Average daily net gain, in kilograms, during—			Station	Average daily net gain, in kilograms, during—		
	July 3 to 15	July 17 to 29	July 31 to Aug. 3		July 3 to 15	July 17 to 29	July 31 to Aug. 3
A-0	0.884	1.011	1.006	E-2	0.923	1.154	
B-0.5	1.020	1.718	1.507	F-3	.735	.690	
D-1.5	.952	1.261	1.148				

TABLE 10.—*Daily average net gain in weight of the colonies at the different stations during the third period, July 31 to Aug. 9, 1929*

Station	Colonies	Average gain per colony, in kilograms, on—							Total of daily average gains in weight	Average daily gain in weight for 10-day period
		July 31	August							
			2	3	5	6	8	9		
	Number								*Kilograms*	*Kilograms*
A-0	13	0.30	2.93	1.71	2.07	1.36	2.17	0.90	11.44	1.144
B-0.5	14	.47	2.97	1.98	2.57	1.57	2.61	.98	13.15	1.315
D-1.5	13	.43	3.47	1.81	1.96	1.05	1.69	.69	11.10	1.110

Table 8 shows that in a majority of cases colonies located at the more distant stations during the second period of 1929 made greater gains in weight when moved nearer the source of nectar. In many instances the average daily gain of such colonies was greater than was that of the colonies at the stations at which the colonies had been consolidated (table 9). In each case the net gain in weight of the colonies was greater at station C-1 than it was after they were moved

within the producing area. This seemed important, as it agreed with the average results obtained in the previous periods.

DISCUSSION OF EXPERIMENTS IN 1927, 1928, AND 1929

The bees from all the stations carried sweetclover pollen during each of the 3 years. The bees at the most distant stations flew at least 8.5 miles before they came to the source of this pollen. Both Caucasian and Italian bees flew this maximum distance.

The average daily net gain or loss in weight of the colonies at the different stations was greater in 1928 than in 1927 or 1929 and also showed more variation between the different stations. These differences cannot be attributed entirely to distance, as some of the colonies at the more distant stations made greater gains than did colonies located at what appeared to be a more favorable distance. The difference was particularly evident between the colonies located at station H-5 and those at station G-4 and was probably due to a difference in the potential or in the actual strength of the colonies at these two stations.

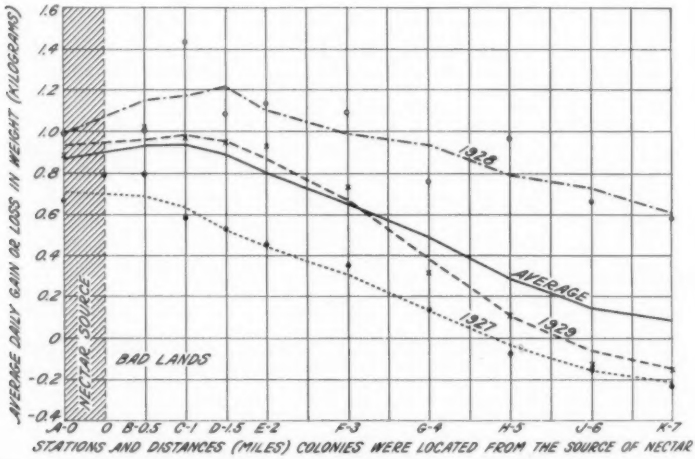


FIGURE 5.—Weight records of the colonies at stations located at known distances from a source of nectar during 1927, 1928, and 1929 in northwestern Wyoming.

The same explanation does not seem to account for the difference in the average daily gain or loss in weight of the colonies within the nectar-producing area and of those located away from the source, as this difference held true during each of the 3 years. The average production of colonies located 1.5 miles from the source of nectar was slightly greater than that of colonies located within the nectar-producing area (fig. 5).

There was a gain of but 0.5 kg (1.1 pounds) in favor of the best Caucasian over the best Italian colony at each of the first 10 stations during the 3 years. This slight difference is hardly indicative of any fundamental difference between the two races in the matter of honey production under the conditions that prevailed during the experiments.

DISTRIBUTION OF HONEYBEES WITHIN A NECTAR-PRODUCING AREA

During the summer of 1930 observations were made on the distribution of bees from apiaries located within nectar-producing areas, to determine, if possible, how far they fly under such conditions and in what manner the bees distribute themselves over the available territory. The observations were made in the San Luis Valley of Colorado and on the plains west of Laramie, Wyo.

The San Luis Valley, with an average elevation of about 7,600 feet, consists of fertile irrigated farming lands devoted to the production of

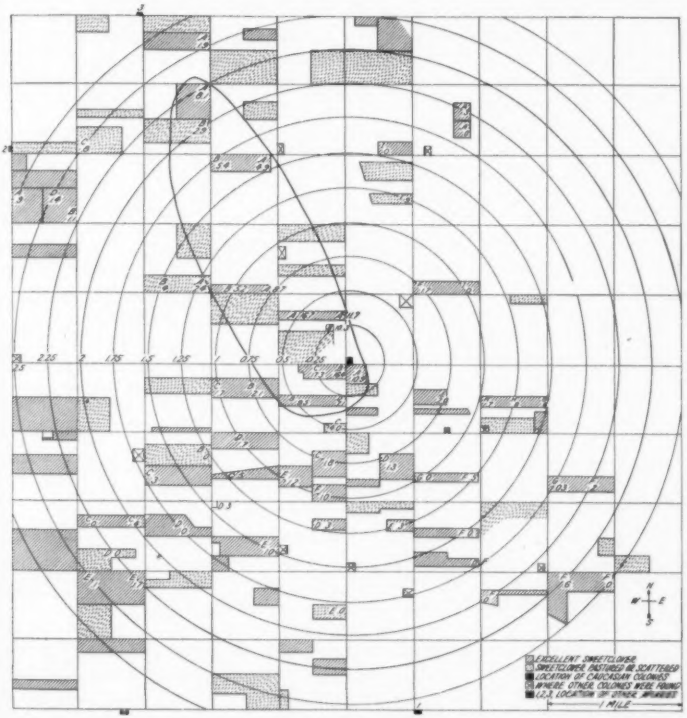


FIGURE 6.—Area in which observations were made on the distribution of bees from a central apiary in the San Luis Valley of Colorado in 1930, showing the average number of Caucasian bees counted in the different sections.

various agricultural crops and to the raising of livestock. Sweetclover is used extensively in the rotation of crops, for hay, pasture, and seed, and forms the principal source of the many carloads of honey annually produced in this valley.

In one section of the valley an area of 25 square miles containing between 2,500 and 3,000 acres of sweetclover was found to be unoccupied by commercial apiaries. Of the few stray swarms found here, all but three were of the Italian race. The location appeared to be not only an excellent place for a commercial apiary but also desirable for carrying on the observations of this experiment (fig.6).

The sweetclover in the many fields varied considerably in height, density of growth, and the stage of bloom during the period of the experiment. Probably 50 percent of the entire stand of clover remained uncut throughout the period in which the observations were being made. Many of the irrigation ditches were lined with a good growth of sweetclover. The fields of clover that had been pastured early in the spring generally came into bloom from 7 to 10 days after the fields that had not been so pastured, and for this reason an attempt was made to indicate in figure 6 the relative importance of the different fields from the standpoint of the density of stand and probable attractiveness to the bees. The fields that were pastured by sheep did not come into bloom until after the bees from the experimental apiary had oriented themselves in relation to the area as a whole.

The location west of Laramie, Wyo., where observations were continued after the close of the work in the San Luis Valley, had a

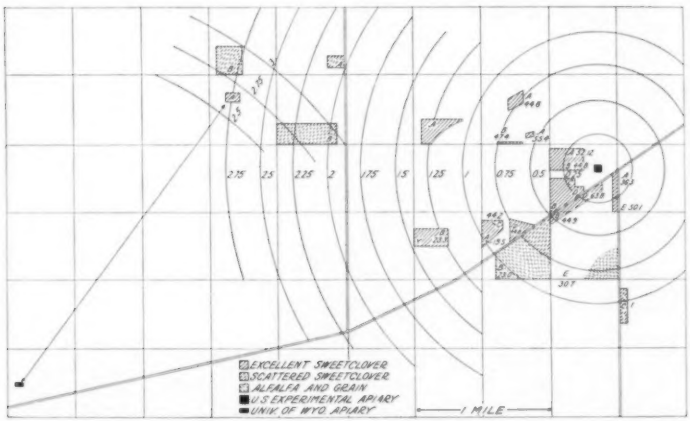


FIGURE 7.—The area in which observations were taken on the distribution of bees from the experimental apiary of the intermountain bee culture field laboratory, near Laramie, Wyo., in 1930, together with the average number of bees counted in different portions of the area. Y at the 1.5-mile point indicates a station at which observations were made, but at which no bees were found.

much more limited range of pasturage, as can be seen readily by comparing figures 6 and 7. The greater portion of this territory, however, was visited almost exclusively by bees from the experimental apiary, consisting of 42 colonies, and from a smaller apiary of 11 colonies situated about 4.5 miles away. The bees from these two apiaries, which were about 2.5 miles apart, worked to a slight extent in the intervening fields of sweetclover.

Since all the stray swarms found within the area in the San Luis Valley and within flying distance of it were Italian bees, with the exception of the three colonies of Caucasian bees mentioned, which were disposed of, it was decided to establish an apiary of Caucasian bees in the center and to use the natural color of the bees as an aid in making the observations. Accordingly, an apiary of 58 colonies, in which most of the bees were well-marked Caucasians, was established in the central position indicated in figure 6. All colonies were manipu-

lated as little as possible and were provided with ample storage space at all times.

To determine the direction of the flight of bees from an apiary, one or more observers walked around it at a distance great enough that the sound made by the bees in the apiary could not be heard. By walking slowly, stopping every few feet to listen for the sound of flying bees and to watch the direction of their flight, it was possible not only to determine the directions in which the bees flew, but also to estimate the relative number flying in any direction.

To determine the distribution of the bees over any given area, three observers took counts of bees as they walked slowly through previously designated fields of sweetclover for a given period of time. Through practice gained by the observers working together before the observations were started and several times during the experiment, it was found that, with the aid of hand tallies, each observer could count the bees in an area approximately 6 feet wide by 60 paces long during a 5-minute period. The observers were assigned to different sectors so that each covered the entire area under observation at one time or another. This procedure tended to equalize the personal equation. The observers took records at the same distances from the apiary and also at the same time, assuring thereby that the observations made at the various distances from an apiary were under identical conditions.

Bees were also marked in the fields with distinctive colors for later identification.

No records were made on days when the wind was blowing, as it was found that bees could not be counted accurately when the sweetclover plants were swaying to any great extent. As the afternoons were generally windy, the counts were for the most part made in the forenoons.

OBSERVATIONS IN THE SAN LUIS VALLEY

The observations taken in the San Luis Valley brought to light much information not anticipated before the work was started. The bees from the experimental apiary oriented themselves the morning after they were established, but no observations were recorded for several days. Most of the sweetclover fields were in good bloom at the time the bees were placed on location. It was soon evident, however, that in spite of the fact that good fields of sweetclover were available on at least three sides of the apiary, with the best fields situated in a southwesterly direction, the bees flew quite generally in a northwesterly lane of flight.[5] A second lane of flight was in a southwesterly direction, while comparatively few bees flew in the other direction.

The data in table 11 and figure 6 indicate that the greatest concentration of bees occurred in the fields adjoining the apiary to the west and northwest and was pronounced for a distance of 0.25 to 0.5 mile. The concentration of bees seemed to be greater in field B, which was adjacent to the apiary on the southwest, than in field A, also adjacent but southeast of the apiary. Only a comparatively few bees were ever found working in the fields southeast of the apiary. The greatest

[5] The term "lane of flight" denotes the direction and manner in which bees fly from an apiary. It is used by many beekeepers, especially in the commercial beekeeping area of the Rocky Mountain region, in a broader sense than the term "line of flight" implies. The latter term is used most frequently to denote the direction and flight of individual bees, or of a swarm, whereas the former denotes the flight of many thousands of bees flying more or less independently but in the same general direction over a narrow angle from the apiary. The two terms are used somewhat synonymously.

concentration of bees was found 0.25 mile west of the apiary, where on an average 17 bees were counted during each 5-minute period. The next greatest concentration occurred in the field 0.5 mile northwest of the apiary (A-0.5). Bees were found in greater numbers in each of five fields northwest of the apiary than in any other fields. The bees were also found to have flown as far as 2.75 miles northwest from the apiary, 2.5 miles southwest, and 2.25 miles to the southeast. The fact that there were at least 1,100 acres of sweetclover in the southwestern quarter of the area, 930 acres in the northwestern quarter, only 220 acres in the northeastern quarter, and approximately 430 acres in the southeastern quarter had little effect on the density of the distribution of the bees.

TABLE 11.—*Distribution of bees in the San Luis Valley of Colorado, in the area shown in figure 6*

Quarter	Station	Counts	Bees	Average bees per count	Quarter	Station	Counts	Bees	Average bees per count
		Number	*Number*	*Number*			*Number*	*Number*	*Number*
Northeastern	F-0.75	7	12	1.7	Northwestern	B-2	12	35	2.9
	I-1	9	0	.0		B-2.25	9	10	1.1
	I-1.25	8	7	.9		A-2.25	11	89	8.1
	I-1.5	9	5	.6		A-2.5	7	13	1.9
	A-1.75	6	0	.0		B-2.5	1	5	5.0
	A-2	6	2	.3		C-2.5	8	6	.8
	A-0	26	284	10.9		D-2.5	15	21	1.4
	E-0.75	4	8	2.0		A-2.75	13	12	.9
	D-0.75	8	10	1.3		B-0	16	362	16.4
	G-1	3	0	.0		C-0.25	23	399	17.3
	H-1	9	4	.4		D-0.25	23	164	7.1
	E-1.25	4	1	.3		B-0.5	22	209	9.5
	F-1.25	2	1	.5		C-0.5	8	32	4.0
	G-1.25	2	0	.0		B-0.75	17	36	2.1
Southeastern	H-1.25	6	5	.8		C-0.75	8	14	1.8
	F-1.5	3	0	.0		C-1	10	7	.7
	G-1.5	7	4	.6		D-1	6	4	.7
	F-1.75	4	0	.0		E-1	6	7	1.2
	G-1.75	26	1	<.1		F-1	4	4	1.0
	E-2	4	0	.0	Southwestern	B-1.25	3	0	.0
	F-2	6	1	.2		C-1.25	2	1	.5
	F-2.25	8	5	.6		D-1.25	4	1	.3
	F-2.5	9	0	.0		D-1.5	12	3	.3
	A-0.25	23	270	11.7		E-1.5	4	4	1.0
	B-0.25	4	41	10.3		C-1.75	3	1	.3
	A-0.5	29	483	16.7		D-1.75	5	0	.0
	A-0.75	23	200	8.7		E-1.75	4	0	.0
Northwestern	B-1	25	129	5.2		C-2	8	3	.4
	A-1.25	5	12	2.4		C-2.25	2	0	.0
	A-1.5	33	161	4.9		D-2.25	4	0	.0
	B-1.5	5	2	.4		F-2.25	6	1	1.7
	B-1.75	33	178	5.4		E-2.5	8	1	.1

The data in table 11 and figure 6 show that beyond a 0.5-mile radius the bees distributed themselves principally in one direction.

The hives in the experimental apiary were located in the southwestern corner of a sparsely wooded pasture and faced south. Adjacent to the apiary at the southwest stood a small group of trees which seemingly did not interfere with the flight of bees. The general direction of the prevailing wind was from the southwest, although at different times it shifted to all other directions. Italian bees were found in all fields in which observations were made, but apparently never in sufficient numbers to be a factor in excluding other bees. No explanation in regard to landmarks, character of the fields, or climatic factors could be found to account for the way in which the

bees distributed themselves in relation to the area as a whole, although the fact that the fields of sweetclover which had been pastured, such as those in which stations B-1.5 and A-1.25 were located, did not come into bloom until after the bees had become oriented undoubtedly was responsible for the low counts.

In another portion of the San Luis Valley a number of apiaries were located in fairly close proximity to one another (fig. 8). As the bees from the experimental apiary mentioned above had not distributed themselves in all directions over the available territory, it

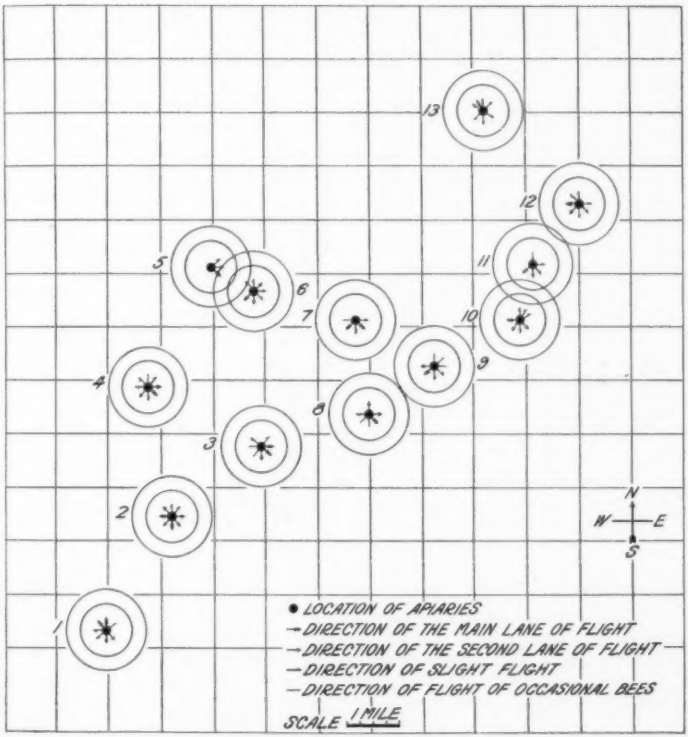


FIGURE 8.—Relative location of 13 apiaries in the San Luis Valley of Colorado, showing the directions in which the bees flew from each apiary.

was thought that a determination of the directions in which the bees flew from the apiaries in another part of the same valley might give some additional information on the distribution of bees when located within a good nectar-producing territory.

It was found that the bees from 9 of the 13 apiaries had only one major lane of flight, and that of the remaining 4 the bees from only 2, nos. 2 and 7, were flying in major lanes of flight that were in different directions. Bees from only two apiaries, nos. 11 and 5, were trespassing within a radius of 1.5 miles in the territory of the major lane of flight of apiaries 10 and 6. In the case of apiary 5 the main

flight went directly over and slightly to one side of apiary 6, so that the bees from apiary 5 were actually working in a territory southeast of apiary 6. The bees from apiary 9 were apparently concentrating their efforts in an area lying between them and that of apiary 8, but as the bees from the latter were flying mainly in another direction the two flights did not cross. In only a few instances, and particularly in the case of apiary 2, were the bees of any apiary taking full advantage of their location, as judged by the directions in which they were working in relation to the fields of sweetclover that surrounded them.

The direction of the prevailing winds appeared to have no definite relation to the principal directions in which the bees were flying from the different apiaries. As the directions of flight evidently depended on a major source of supply to which the bees had oriented themselves at the time the plants came into bloom, it is only reasonable to suppose that the direction of flight would depend on a continuance of the nectar flow in that direction. If for any reason the source of food was reduced or if a better source of nectar was discovered in another direction, the direction of flight might be changed accordingly.

Such a contingency was investigated by the writer during the summer of 1929. For some unexplained reason, at certain times nearly every summer bees from a commercial apiary near Worland, Wyo., were in the habit of leaving a fertile valley in which they were located to fly over a stretch of badlands to a much smaller valley and bring back nectar in quantity and quality similar to what they had been gathering. The distance across the badlands was 4.6 miles. On other occasions, however, the bees had been observed to fly in a slightly different direction, making the distance covered even greater. In order to leave the valley in which they were located, the bees had to fly over a steep rise of land that was estimated to be at least 150 feet higher than the apiary. The badlands were extremely rough, there was no source of water or nectar between the two valleys, and the flight was not in the direction of the prevailing winds.

OBSERVATIONS NEAR LARAMIE, WYO.

As stated previously, the nectar-producing flora in the vicinity of the apiary west of Laramie, Wyo., belonging to the intermountain bee culture field laboratory, was much more limited than that in the San Luis Valley of Colorado; consequently, the observations were confined to a smaller area (fig. 8). The distribution of the bees was found to be somewhat uniform within a radius of 0.75 mile, but beyond this distance the number of bees found in any field decreased considerably, as did also the available sources of nectar. Field A-1.25 and the greater portion of B-1.5 were cut for hay soon after the observations were started. Field B-2 was in good bloom but consisted of very short clover that had not been irrigated and, although it was examined on several occasions, no bees were ever found there. Only a few bees were found in field A-2.75 and in B-2.75, but most of these were shown to have come from the apiary of the University of Wyoming, 2.5 to 2.75 miles to the southwest.

As the colonies in this location were stronger than those in the experimental apiary in the San Luis Valley, the results of the two sets

of observations cannot be compared directly. Possibly this factor, plus the restricted territory of the Laramie location, was responsible for the noticeable increase in the numbers of bees found working in the areas under observation.

DISTRIBUTION OF MARKED BEES

A number of bees were marked distinctive colors in each of the 3 fields in the San Luis Valley and in 3 fields west of Laramie, in an attempt to identify the colonies from which they came and thus to establish the distances they flew, and also to learn whether the same bees return to the same fields on successive days.

In field D-1.5 in the San Luis Valley 150 bees were marked with a green dot. On four successive days thereafter green-marked bees were found in the same field. A beekeeper told the writer that he had found 2 green-marked bees in his apiary 2.5 miles southeast of this field 2 days after the bees were marked. No green-marked bees were ever found in the experimental apiary.

In one corner of a much larger field, B-1.75, 190 bees were marked another color. Over a period of 12 days thereafter some of these marked bees were found working in the same small corner of the field in which they were marked. During the same period 12 bees with the same markings were found in the experimental apiary, and 1 was found working in field A 7 days after the first bees were marked.

In a third field, A-2.25, 10 bees were marked still another color and, although none of these were ever found again in the same field, 4 of them were seen in the hives of the experimental apiary on the third, sixth, and eighth days after they were marked.

In an effort to determine from which apiary the bees came that were found working in field A-2.5 (fig. 7) near Laramie, 126 Caucasian and 42 Italian bees were marked in that field. Two days later, when only a few bees were working, 3 marked bees were seen in the same field. On the following day 1 of the marked bees was found in the apiary connected with the intermountain bee culture field laboratory and 47 in the apiary belonging to the University of Wyoming. These 47 bees were scattered in 10 of the 11 colonies in this apiary, although in 1 colony 25 marked bees were counted.

In another small field located beyond the flying range of these 2 apiaries but within 2.5 miles of 5 other apiaries, which ranged from 6 to 37 colonies in size, 827 bees were marked. During a 30-minute examination of this field on each of 2 successive days thereafter, 36 marked bees were observed out of a total of 493 bees counted. The colonies in the 5 apiaries were then searched, with the result that marked bees were found in each apiary, and a total of 127 marked bees were located (table 12). Although 7 colonies of bees were found in the field in which these bees were marked, only 22 marked bees were recovered in these colonies, in contrast to 31 in the same number of colonies 0.5 mile west of the field. In another apiary 2.25 to 2.5 miles distant, from which the bees had to fly over the city of Laramie, Wyo., as well as over a mile or more of other territory, in order to reach the small field of clover, 5 marked bees were recovered.

TABLE 12.—*The distribution of bees from 5 apiaries in relation to a small field in which 827 bees were marked*

Distance of apiaries from field (miles)	Colonies in apiary	Colonies examined	Colonies with marked bees	Bees found in each colony (number)	Total marked bees found
	Number	*Number*	*Number*		*Number*
Same field	7	7	7	6, 4, 2, 2, 3, 2, 3	22
0.5	7	7	7	1, 6, 2, 6, 4, 6, 6	31
0.75	43	37	11	1, 1, 1, 1, 1, 3, 1, 1, 1, 2, 1	14
1.25 to 1.5	29	23	9	1, 12, 3, 1, 28, 1, 4, 3, 2	55
2.25 to 2.5	7	6	3	1, 2, 2	5

SUMMARY

Estimates of various writers have placed the flight range of honeybees at distances of from 1 to 7 or more miles, but little experimental evidence has been presented. It is also generally believed by beekeepers that bees will fly in all directions from an apiary in quest of nectar and pollen. Regulations governing the location of apiaries in respect to the control of bee diseases, from the viewpoint of honey production, and to prevent bees from becoming nuisances, vary widely in their requirements owing to differences in the assumed distances that bees can fly.

When colonies were located on a prairie in Wyoming, during a dearth of nectar, it was found that the bees would fly but 1.5 miles for artificial stores and at least 3 miles for pollen and nectar.

When bees were separated from a given nectar-producing area by the badlands, with no other source of food intervening, they flew a maximum distance of at least 8.5 miles. Colonies located within 0.5 to 2 miles of a given source of nectar made gains in weight, over a period of 3 years, as great as, or greater than, similar colonies located within the same nectar-producing area, and colonies lost in weight when placed 5 miles or more from nectar.

When colonies were moved for varying distances up to 3.5 miles, many bees went to the fields and then returned to their former locations. The return of such bees was undoubtedly influenced by the fact that the colonies had been moved into surroundings that were similar to their former locations and also by the fact that the bees worked in the same territory in which they had worked before being moved.

Experiments on the distribution of bees from apiaries located within a nectar-producing area showed that bees have a tendency to fly in only one or two major lanes of flight, neglecting similar forage plants in other directions. Bees would fly for 2.75 to 4.6 miles in one direction when located within a nectar-producing area and confine their efforts to working in that direction rather than in nearer fields of seemingly equal attractiveness. In one series of observations, bees were found to work most numerously in fields located within 0.5 mile of their apiary. Where several apiaries were located within the same general territory, the major lanes of flight from the different apiaries did not indicate so much trespassing of the bees from any one apiary on the territory of another as might be expected from the proximity of their locations. Where the nectar supply was limited, bees from

several colonies in each of five apiaries worked in the same small field, some of the bees flying at least 2.5 miles to reach the field in question.

The results confirmed the conclusions of previous investigators that bees have a tendency to return to the same portion of a field, or to the same small field, on successive days for nectar and pollen, even though other areas of the same forage plant are nearer.

LITERATURE CITED

(1) ANONYMOUS.
1927. THE BEE AND HER LOAD. HOW FAR DOES SHE TRAVEL? New Zealand Smallholder 10 : 92.

(2) BUTTEL-REEPEN, H. v.
1915. LEBEN UND WESEN DER BIENEN. 300 p., illus. Braunschweig.

(3) DADANT, C. P.
1922. LE SYSTÈME DADANT EN APICULTURE. 138 p., illus. Quebec.

(4) [HILLMAN, D. H.]
1929. COPY OF PROPOSED REGULATIONS FOR SHIPPING OF BEES INTO UTAH. REFERRED TO THE COMMITTEE ON IRRIGATION AND AGRICULTURE, 1929. Western Honeybee 17 (3): 18.

(5) HUISH, R.
1844. BEES: THEIR NATURAL HISTORY AND GENERAL MANAGEMENT: COMPRISING A FULL AND EXPERIMENTAL EXAMINATION OF THE VARIOUS SYSTEMS OF NATIVE AND FOREIGN APIARIANS; WITH AN ANALYTICAL EXPOSITION OF THE ERRORS OF THE THEORY OF HUBER; CONTAINING, ALSO, THE LATEST DISCOVERIES AND IMPROVEMENTS IN EVERY DEPARTMENT OF THE APIARY. New ed., greatly enl., 458 p., illus. London.

(6) HUTCHINSON, W. Z.
1891. ADVANCED BEE-CULTURE, ITS METHODS AND MANAGEMENT. 87 p., illus. Flint, Mich.

(7) HUTSON, R.
1926. RELATION OF THE HONEYBEE TO FRUIT POLLINATION IN NEW JERSEY. A PRELIMINARY REPORT. N.J. Agr. Expt. Sta. Bul. 434, 32 p., illus.

(8) MILLER, C. C.
1917. A THOUSAND ANSWERS TO BEEKEEPING QUESTIONS. 276 p., illus. Hamilton, Ill.

(9) SHEPPERD, J. H.
1927. SWEET CLOVER EXPERIMENTS IN PASTURING. N.Dak. Agr. Expt. Sta. Bul. 211, 56 p., illus.

(10) UNITED STATES RECLAMATION SERVICE.
1922. SHOSHONE IRRIGATION PROJECT IN WYOMING. Map No. 18999A.

(11) WAITE, M. B.
1899. POLLINATION OF POMACEOUS FRUITS. U.S. Dept. Agr. Yearbook 1898: 167–180.

METHODS OF CONTROLLING POLLINATION IN THE PECAN[1]

By HAMILTON P. TRAUB, *horticulturist*, and L. D. ROMBERG, *agent, Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture*

INTRODUCTION

A workable method for the control of pollination in the pecan is a prerequisite to further progress in the study of pollination problems and in the prosecution of practical breeding work. Various methods have been employed by different workers in an attempt to control pollination in the pecan. Risien (*3, 4*)[2] first used large paper bags for covering the pistillate flowers. The bags were tied on the twig below the new growth. Later he used small gelatin capsules, pushing them over the pistillate clusters and stuffing the open end with cotton. This method was not satisfactory because the capsules softened when wet. He also used small electric light bulbs which were fastened to a support to lessen the weight on the shoot. Stuckey (*5*) used closely woven lawn cloth bags; Adriance (*1*) used glassine bags; and Reed (*2*) used "medicated" cotton covers, a method previously employed by Van Fleet.

In 1930 Woodroof (*7*) pointed out that apparently all the work done up to that time on the control of pollination in the pecan was open to question because of the failure to prove definitely that foreign pollen had been excluded. The experiments herein reported were therefore undertaken to devise, if possible, a more effective method for controlling pollination in the pecan.

MATERIAL AND METHODS

The trees used in the experiments were located in the Pearce pecan orchard on the Colorado River near Austin in central Texas and in the Kemper pecan orchard on the Red River near Denison in northeastern Texas[3] (fig. 1).

The method finally adopted for excluding pollen was to cover the pistillate terminal with a finely woven cloth bag dipped in boiling paraffin of low melting point. In such a bag the qualities of pliability, durability against winds and rain, transparency to light, relatively light weight, and capacity to exclude wind-carried pollen effectively were apparently obtained in sufficient measure. This fundamental method was used in several variations and was checked against the commonly used cotton-cover method. The types of covers tested were as follows:

(1) Large nonventilated paraffined cloth bags (fig. 2, A).—A commercial mailing sack, 6¾ by 13½ inches, was pulled over the shoots of the twig, and the neck of the bag was securely tied to the twig. The string was drawn together at two or three places over a space of about 1 inch to reduce the possibility of pollen entering at that point.

[1] Received for publication Mar. 13 1933; issued September 1933.
[2] Reference is made by number (italic) to Literature Cited, p. 296.
[3] The experiments at Denison, Tex., were carried on cooperatively with the Texas State Department of Agriculture.

(2) Large ventilated paraffined cloth bags (fig. 2, B).—Bags similar to those just described were used, but ventilation was provided. This was accomplished in two ways. In one set of tests a corner of each bag was cut out and filled with a cotton plug and the neck of the bag was tied down on a cotton layer about 1½ to 2 inches in diameter. In the other tests ventilation was provided only by means of a cotton layer in the neck of the bag.

(3) Small nonventilated paraffined cloth bags.[4]—These bags measured 1⅝ by 3⅜ inches when flattened out, and when opened were approximately 1 inch in diameter. Some were attached by tying the neck with a string only; others by tying in the same manner but thereafter sealing the neck with melted paraffin.

(4) Small ventilated paraffined cloth bags (fig. 2, C and D).—These bags were identical with those just described, but when they were attached the neck of each was stuffed with cotton, which not only provided ventilation but also acted as padding for the tender shoot. One leaf was usually pinched off to make room for the cotton padding, and 2 to 5 of the small young leaves immediately below the blossoms were placed in the bag. A pad of cotton was wrapped around the shoot at the selected point, and the open bag was pushed over the pistillate cluster, terminal leaves, and cotton. The bags were put on as far out on the

FIGURE 1.—Typical pecan trees used in the experiments: A, Tree 25 feet high in Kemper orchard, Denison, Tex.; most of work done from the ground; B, Tree 40 feet high in Pearce orchard, Austin, Tex.; note 22-foot ladder necessary to carry on work.

tender shoots as possible without tilting the shoot downward too much. The tendency to droop was overcome as the shoots grew stronger. Two methods were used in fastening the bags. Half of the bags for each treatment were lightly stuffed in the neck with cotton and were secured by a string tied around the neck (fig. 2, D). The other half were fastened by using cotton stuffed tightly enough into the neck of the bag to hold it in place without tying (fig. 2, C).

(5) Cotton covering.—From large bundles of commercial quilt cotton whole layers about 1 inch thick (loose) were taken off. Pieces 3 to 4 inches square were torn from these layers and made into covers by rounding and thinning the edges and pushing the sides together over the fingers so as to form a cup-shaped or bag-shaped mass. The cover was pushed over the terminals and tied below the blossoms and outermost leaves with a string. The cotton surrounding the blossoms was one half to three fourths of an inch thick, forming a ball 1½ to 2 inches in diameter on the shoot (fig 2, E). Usually it was necessary to remove a leaf from the shoot to facilitate the tying of the cotton in place.

Two methods of applying pollen, designed to exclude foreign pollen, were employed in the experiments, viz, (1) the use of a hypodermic

[4] The value of cellophane bags for this purpose is being tested.

FIGURE 2.—Types of covers used in pollination tests: A, Large nonventilated paraffined cloth bag; B, large ventilated bag; C, small ventilated bags, not tied; D, small ventilated bags, tied; E, cotton cover.

syringe (fig. 3) which made it unnecessary to remove the bag, and (2) the application of the pollen after removal of the bag, at an hour of the day when there was little possibility of pollen being carried in the air, and immediate replacement of the bag. When the syringe was used, the needle was thrust through the paraffin-impregnated cloth and the pollen injected into the bag. Immediately after the needle was withdrawn the punctures were closed by smearing with paraffin of low melting point. In the case of the small ventilated bags the needle was inserted either through the cotton pad or as previously indicated.

It has been shown that no pecan pollen is shed when the relative humidity of the air is 85 percent or higher (*7*). Actual tests with petrolatum-coated glass slides supported on a rack after the method used by Waugh (*6*) and Woodroof (*7*) indicated that there was little or no pollen in the air between the hours of 5 and 7 a.m. It appeared safe, therefore, to carry on the operations between these hours. In certain tests, bags were removed after 7 a.m. to determine the probability of contamination and whether pollination later in the day would affect the set.

FIGURE 3.—Syringe used in pollinating.

In order to get a controlled cross it is necessary to procure uncontaminated pollen. A promising method consists in picking the catkins before any pollen has been shed, washing them repeatedly in water between the hours of 5 and 7 a.m., and drying them in a desiccator after the excess water has been removed with a sterile towel. After the pollen is shed in the desiccator it is run through a fine-mesh sieve to remove larger particles. The pollen is then stored in glass vials stoppered with cotton and covered with a vial of larger size. The quantity desired in the pollen container of the syringe is sucked through the hypodermic needle after the needle has been thrust through the cotton plug. When the variety of pollen is to be changed both the sieve and the entire syringe are sterilized by the use of 95 percent ethyl alcohol. This method was not followed throughout in the preliminary work, since the question of making a particular cross was not involved.

In part of the work the hypodermic syringe employed was the type ordinarily used by physicians, but this was not entirely satisfactory for the purpose. It was therefore modified by putting on a large rubber bulb such as is used on syringes to fill automobile batteries. This bulb, which served as a container for the pollen, held a sufficient quantity for a large number of pollinations. Other improvements in the syringe which will allow the insertion of the needle at any angle and also provide a constant quantity of pollen, are now under consideration.

The various treatments consisted in utilizing the types of covers described and pollinating by needle injection; also, by removal of the covers at an hour when there was little or no pollen in the air and subsequent replacement of the covers. Check treatments included covers that were not removed for the bagging period and covers that were removed for a time equivalent to that required for pollination and then replaced. In two instances the covers were removed and pollen applied after 7 a.m., with replacement. At the time when these treatments were given, some covers were removed permanently.

Records of the number of clusters and the number of nuts per cluster were taken (1) when the bags were finally removed, (2) in early July, (3) in August, and (4) at the time of harvesting. When the July check was made, bags of mosquito netting were placed over the clusters to protect them from further damage by casebearers and to catch any nuts that might drop. At this time it appeared that all nuts that might drop owing to lack of fertilization were off. Later much damage to the nuts at the Red River orchard was caused by a severe storm and by scab. Conclusions as to results of the different methods must therefore be based chiefly upon the July data.

PRESENTATION OF DATA

The results of the experiments are presented in tables 1 and 2.

TABLE 1.—*Results of experiments with different methods for controlling pollination in the pecan in Texas in 1931*

KEMPER ORCHARD AT DENISON

Variety, tree, and kind of bag or cover	Bags or covers originally placed	Bags or covers usable	Bags or covers per treatment	Nature of treatment	Date bags or covers were originally placed	Date treatment given	Date bags or covers were permanently removed	Clusters in usable bags when bagged [a]	Clusters when bags or covers were removed	Nuts when bags or covers were removed	Nuts on tree July 1		Data on nuts Aug. 18				Nuts harvested Oct. 22
													Destroyed by storm	Destroyed by caseBearer	Dropped	On tree	
Halbert (tree no. 96):	*No.*	*No.*	*No.*					*No.*	*No.*	*No.*	*No.*	*Pct.*	*No.*	*No.*	*No.*	*No.*	*No.*
Large nonventilated bag	121	119	21	Check; not pollinated; neck not paraffined	May 3		May 31	48	29	74	0	0				0	0
			20	Check; not pollinated; neck paraffined	do		do	39	19	45	0	0				0	0
			20	Pollinated by needle injection	do	May 16	do	49	21	64	0	0				0	0
			20	Removed; pollinated; replaced; before 7 a.m.	do	May 17	do	44	28	67	4	6	0	0	0	4	3
			20	Removed; not pollinated; replaced; before 7 a.m.	do	do	do	46	19	44	0	0					
			18	Bags removed and left off	do		May 18	38	14	33	14	42	2	0	0	13	13
Halbert (trees nos. 265, 211, and 246):																	
Large ventilated bag	60	59	20	Check; not pollinated	May 6, 7		June 1	52	44	136	0	0				0	0
			20	Pollinated by needle injection	do	May 16	do	57	39	112	13	11	7	0	0	6	6
			19	Removed; pollinated; replaced; before 7 a.m.	May 7	May 17	do	59	54	184	20	11	13	2	2	3	2
Halbert (trees nos. 211 and 179):																	
Small ventilated bag, tied	40	40	10	Check; not pollinated	May 4		do	10	9	30	0	0				0	
			11	Pollinated by needle injection	do	May 16	do	11	11	32	25	78	0	0	0	25	[b] 23
			10	Removed; pollinated; replaced; after 7 a.m.	do	May 17	do	10	9	27	18	66	0	0	0	18	[c] 16
			9	Removed; not pollinated; replaced; after 7 a.m.	do	do	do	9	9	24	2	8	0	0	0	2	2
Small ventilated bag, not tied	40	40	11	Check; not pollinated	do		do	11	11	40	0	0				0	0
			9	Pollinated by needle injection	do	May 16	do	9	8	30	15	50	2	3	0	9	9
			10	Removed; pollinated; replaced; after 7 a.m.	do	May 17	do	10	7	23	16	70	15	0	0	1	1
			10	Removed; not pollinated; replaced; after 7 a.m.	do	do	do	10	9	36	1	3	0	0	0	1	0
Summary of small bags both tied and not tied	80	80	21	Check; not pollinated	do		do	21	[d] 20	70	0	0				0	0
			20	Pollinated by needle injection	do	May 16	do	20	[d] 19	62	40	64	2	3	0	34	32
			20	Removed; pollinated; replaced; after 7 a.m.	do	May 17	do	20	[d] 16	50	34	68	15	0	0	19	17
			19	Removed; not pollinated; replaced; after 7 a.m.	do	do	do	19	[d] 18	60	3	5	0	0	0	3	2
Halbert (trees nos. 324 and 265):																	
Cotton	60	49	14	Check; not pollinated	do		May 31	14	11	47	26	55	1	0	0	25	21
			18	Removed; pollinated; re-covered	do	May 18	do	18	18	61	53	87	0	0	1	52	52
			17	Removed; pollinated; left uncovered	do	do	May 18	17	16	58	50	86	0	0	1	49	48

PEARCE ORCHARD AT AUSTIN

Success:																		
Large nonventilated bag	100	100	40	Check; not pollinated	Apr. 27		June 4		31		[a] 0	[a] 0				[a] 0	(f)	
			20	Pollinated by needle injection	do	May 17	do		23		0	0				0		
			20	Removed; pollinated; replaced; before 7 a.m.	do	do	do		16		3	19		[c] 3		0		
			20	Removed; not pollinated; replaced; before 7 a.m.	do	do	do		27		0	0				0		
Large ventilated bag	60	60	20	Check; not pollinated	May 2		do		22		0	0				0		
			10	Pollinated by needle injection	do	May 17	do		8		0	0				0		
			10	Removed; pollinated; replaced; before 7 a.m.	do	do	do		9		1	11		1		0		
			20	Removed; not pollinated; replaced; before 7 a.m.	do	do	do		27		0	0				0		
Small nonventilated bag, neck not paraffined.	40	37	10	Check; not pollinated	May 8		do		10		0	0				0		
			7	Pollinated by needle injection	do	May 16	do		7		3	42				3		
			10	Removed; pollinated; replaced; before 7 a.m.	do	do	do		5		2	40				2		
			10	Removed; not pollinated; replaced; before 7 a.m.	do	do	do		9		0	0						
Small nonventilated bag, neck paraffined.	40	19	10	Removed; pollinated; replaced; before 7 a.m.	do	do	do		9		0	0				0		
			9	Removed; not pollinated; replaced; before 7 a.m.	do	do	do		5		0	0				0		
Cotton	110	78	20	Check; not pollinated	May 1		do		16		5	31				5		
			20	Removed; pollinated; replaced; before 7 a.m.	do	May 16	do		20		5	25				4		
			20	Removed; not pollinated; replaced; before 7 a.m.	do	do	do		18		7	38				7		
			18	Removed and left off	do	do	May 16		18		10	55				10		
Burkett:																		
Large nonventilated bag	30	30	30	Not pollinated	Apr. 19		June 4		7		0	0				0		

[a] As a rule, when large bags were used several shoots were enclosed.
[b] In addition, 3 much undersized empty shells were found.
[c] In addition, 2 much undersized empty shells were found.
[d] Of the 7 missing clusters, 2 were abscised and 5 were broken off together with bag.
[e] This column is based on number of clusters.
[f] No further data taken.

TABLE 2.—*Loss of nut clusters from covered shoots*

Type of cover	Halbert variety (Kemper orchard) [a]			Success variety (Pearce orchard); abscission during 30 days after removal [a]
	Abscission while bagged	Abscission during 30 days after removal	Total	
	Percent	*Percent*	*Percent*	*Percent*
Large nonventilated bag	36	57	93	81
Large ventilated bag	7	76	83	80
Small nonventilated bag (not paraffin-sealed)				60
Small ventilated bag	0	6	6	
Cotton	0	0	0	75

[a] The percentage of abscission for the Pearce orchard is based on the number of clusters on the tree at cover removal; for the Kemper orchard it is based on the number when first covered. The data are only for those clusters that were in the group to be pollinated by removal of covers.

In a consideration of the effect of the bags on the shoots, the length of the time of bagging and the effect of the size and ventilation of the bags are important. Apparently a valid criterion for pistil receptivity in the pecan has not yet been demonstrated (*7*, *5*, *1*). For this reason it was difficult to determine how long the bags should remain on, and they may possibly have been left on longer than was actually necessary. As would be expected, growth was stimulated in the shoots bagged during the early part of the season (from the middle to the end of April), which was relatively cool. However, as the warmer weather of May came on, there seemed to be a reversal of this process, and a retarding effect was noticed. In all bags a shedding of foliage was observed, due apparently to the changed environmental conditions caused by the cover. A tendency of the young nuts to abscise seemed to be positively correlated with injury to the foliage. After the bags were removed the shedding of foliage ceased, but the young nuts continued to abscise abnormally in proportion to the abscission exhibited during the bagging period. In the case of the large bags placed on the Success variety at the Pearce orchard, approximately 10 percent of the bagged shoots produced staminate flowers from lateral buds which would not normally have been produced until a year later. In several cases pistillate flowers were borne on these staminate inflorescences intermingled between the staminate florets. Cotton covers gave varying results at the two orchards, possibly owing to the difference in varieties or in the application of the material.

A summary of the data on the loss of clusters and nuts from shoots while covered and during 30 days after removal of covers of properly pollinated clusters is given in table 2. It will be noted that ventilation is apparently beneficial,[5] and also that a small cover enclosing only the terminal portion of the shoot is apparently less harmful than a large one enclosing the entire shoot. Some abscission of nutlets is known to occur where clusters have not been bagged. For this reason the abscission from clusters covered with small ventilated bags does not appear to be excessive; for large bags, both ventilated and nonventilated, abscission is relatively high. It may be, however, that when a valid criterion for pistil receptivity is found, the length

[5] Water collected in the lower end of nonventilated bags.

of time necessary to cover may be reduced to such an extent that all types of covers will be less harmful. By referring to table 1 it will be noted that the treatment of large nonventilated bags, which consisted in removing the bags permanently after 15 days, gave a 42 percent set of nuts, whereas under similar bags removed after 28 days, a set of only 6 percent occurred. In the latter case the flowers had been artificially pollinated.

In considering the degree of control secured by the various treatments, the effect of pollinating and of not pollinating, the relative effectiveness of pollinating by means of a hypodermic syringe and pollinating by removal of the cover, the relative value of the bagging methods as contrasted with the cotton method, and any indication of self-sterility or intersterility should receive attention. As shown in table 1, complete control was secured in every case where the bagging technic was employed and pollen was withheld. Similarly, nuts were set in the majority of cases where pollination was artificially attempted. Apparently there is no consistent difference in the number of sets due to the use of the syringe in pollinating and to the use of the method of removing, pollinating, and replacing before 7 a.m. (table 2). Some nuts were set on clusters similarly exposed after that hour, when pollen was known to be in the air. Partial control of fertilization was secured with cotton covers. Fewer nuts were set in clusters not artificially pollinated and continuously covered than in clusters that were artificially pollinated.

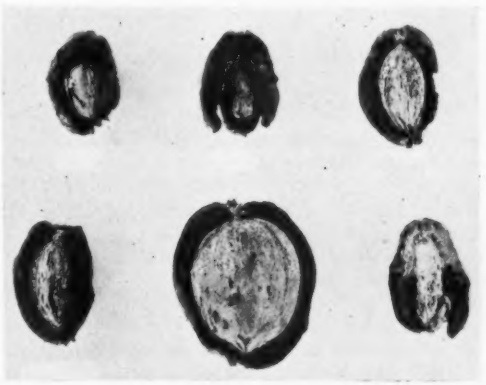


FIGURE 4.—Normal and abnormal Halbert pecans from self-pollinated clusters; harvested October 22. The large nut (lower center) is normal; the nut to its left is an abnormal one from the same cluster. The others are abnormal nuts from different clusters.

The relative value of the small bags, large bags, and cotton covers must be judged both by the effect of the covers on the shoots and by the degree of control secured. On this basis the small ventilated bags appear to be decidedly superior to the large bags whether ventilated or not ventilated. Cotton covers as used in this experiment allowed pollen to sift through. Birds removed some for nest building. Cotton covers are also less desirable than small ventilated bags because they do not permit pollination by needle and because much more work is required to place them on the trees, to remove them for pollination, and to replace them. With walnut work on the Pacific coast a more careful cotton-cover technic is employed, which apparently is more effective than the method used in these experiments.

Pollen from Halbert trees was used throughout this experiment. No arrested or abnormal nut development was observed except with the Halbert variety (fig. 4), which would indicate that this variety may be somewhat self-incompatible.

CONCLUSIONS

The results of one season's work carried out at two locations in Texas indicate that—

(1) The requirements of an effective covering material apparently are met by the use of a finely woven cloth impregnated with paraffin of low melting point.

(2) Controlled pollination may be effected by means of a hypodermic syringe, without removing the covers.

(3) Controlled pollination may be effected by pollinating after removing the cover and then replacing it between the hours of 5 and 7 a.m. (relative humidity 85 percent or above), under the conditions of this experiment.

(4) Cotton covers as used in the experiments gave no effective control.

(5) The use of a small paraffined cloth bag with cotton stuffed into the neck to provide ventilation and padding for the tender shoot, and pollinating by means of a hypodermic syringe give promise of excellent control easily secured, if one season's results are verified in future years. This type of cover is in every way superior to the large ventilated bag.

LITERATURE CITED

(1) Adriance, G. W.
1931. Factors influencing fruit setting in the pecan. Bot. Gaz. 91: 144–166, illus.

(2) Reed, C. A.
[1929]. Pecan pollination and breeding investigations by the United States Department of Agriculture. Natl. Pecan Growers' Assoc. Bul. 2: 140–145.

(3) Risien, E. E.
1904. Pecan culture for western Texas. 55 p., illus. San Saba, Tex.

(4) ———
1908. Hybridizing the pecan. Tex. Dept. Agr. Bul. 2: 26–27.

(5) Stuckey, H. P.
1916. The two groups of varieties of the hicoria pecan and their relation to self-sterility. Ga. Agr. Expt. Sta. Bul. 124, p. [127]–148, illus.

(6) Waugh, F. H.
1901. Report of the horticulturist. Vt. Agr. Expt. Sta. Ann. Rpt. (1899–1900) 13: 333–373, illus.

(7) Woodroof, J. G.
1930. Studies of the staminate inflorescence and pollen of hicoria pecan. Jour. Agr. Research 40: 1059–1104, illus.

BLISTER RUST DAMAGE TO NORTHERN WHITE PINE AT WATERFORD, VT.[1]

By E. C. FILLER[2]

Senior pathologist, Division of Blister Rust Control, Bureau of Plant Industry, United States Department of Agriculture

INTRODUCTION

White-pine blister rust, caused by the fungus *Cronartium ribicola* Diet., was first found in North America during 1905 in a nursery near Philadelphia, Pa. (*6*).[3] Subsequent investigations have indicated that it was introduced in York County, Maine, as early as 1897, on European black currants (*Ribes nigrum* L.) imported from England (*7*). However, far more important introductions occurred as the result of importations of northern white pine (*Pinus strobus* L.) from European nurseries during the period from 1900 to 1910. Surveys have shown that diseased stock was planted in more than 200 locations in the Northeastern States. From these infection centers the blister rust spread to natural stands of white pine through the medium of ribes [4] and thus became generally distributed in these States (*9*).

In the Northeast blister rust has seriously endangered the survival of white pines wherever they occurred closely associated with ribes, the alternate host of the fungus. White pines of all sizes are attacked and killed by the rust (*10*), but the time required for killing is proportionate to the size of the tree. Consequently, on many areas in the older infested regions, where the trees have not been protected by the timely eradication of ribes, the seedling pines have already been killed and the sapling growth has been severely injured, as shown by the many dead and dying trees, while among the merchantable-size trees the damage is only now beginning to accrue. Except for the presence of dying branches, the effect of the disease on the larger pines does not become readily noticeable until the girdling of the trunk causes the crown foliage above to turn yellow. In the case of large trees under eastern conditions, this sometimes requires 15 years or more. So insidious is its attack that frequently the blister rust progresses to this advanced stage before it is recognized by pine owners.

The blister rust was first found in northern Vermont in 1910. Survey records indicate that it was introduced there on northern white pine imported from Germany about 1901 and planted at Lyndonville. From this and from later plantings of infected pines imported in 1909 the disease became generally distributed in the native white pine areas of this district.

[1] Received for publication Jan. 26, 1933; issued September 1933, Cooperative investigations by the U.S. Department of Agriculture and the infested States.

[2] The field data on wild ribes and pines in the pasture pine type were secured in 1924 under the direction of E. R. Ford, formerly of the Division of Blister Rust Control; the data for the merchantable stand were obtained under the supervision of the writer and represent conditions existing in 1925 and 1930. The writer wishes to acknowledge his indebtedness to the staff of the Washington office, Division of Blister Rust Control, for assistance in preparing the manuscript.

[3] Reference is made by number (italic) to Literature Cited, p. 313.

[4] When not employed as a generic name, the term "ribes" is used in this paper to designate currant and gooseberry plants.

An investigation was begun in 1924 on an area at Waterford, Caledonia County, Vt., where considerable blister rust damage was beginning to occur among white pines of merchantable size. In order to prevent additional infection, initial control measures were applied in 1925. This work consisted of uprooting the ribes on and near the area. Although this procedure established control of the disease, it was of course no deterrent to the continued growth and killing action of the cankers that had originated prior to the eradication of the ribes.

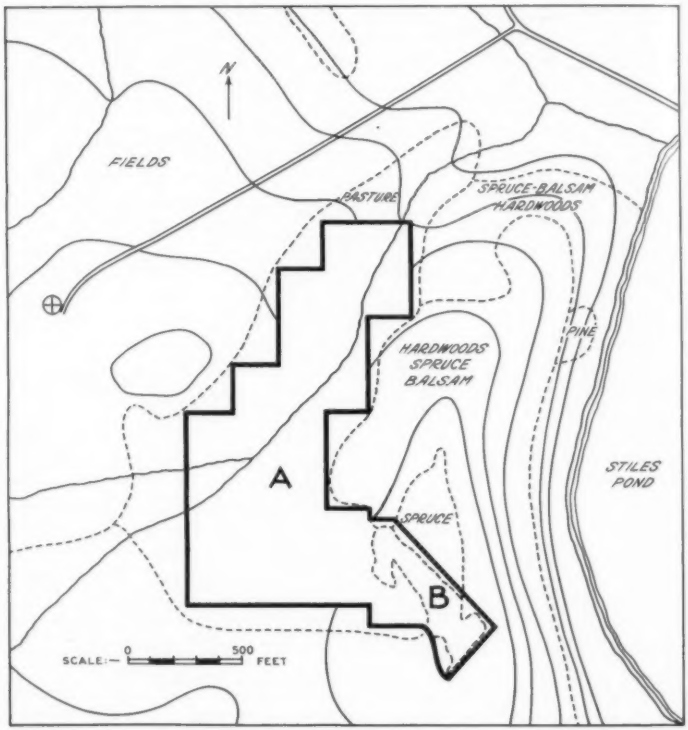


FIGURE 1.—Sketch map of study area at Waterford, Vt.[8] Heavy black line indicates boundary of study area: A, Pasture-pine type; B, merchantable-pine type. Continuous lines (———) represent contours (40-foot intervals); wavy lines (~~~~), streams; broken lines (·····), type boundaries; double lines (═══), roads. The symbol ⊕ indicates location of cultivated black currants.

Data obtained during this investigation, on the occurrence and effect of blister rust on merchantable white pine, are presented in this paper.

DESCRIPTION OF INFESTED AREA

The area studied comprises 27.43 acres located on the top and on the northeastern slope of a rolling upland plateau (fig. 1). It contains two forest types: (1) A scattered stocking of uneven-aged, bushy white pines in an old pasture of 25 acres, where in 1924 there was an

[8] Details of types and topography were taken from a sketch map prepared by A. E. Fivaz in 1927.

average of 72 trees per acre, ranging up to 50 feet in height; and (2) a 2.43-acre mixed stand of 60-year-old white pines, uneven-aged spruce, and hardwoods. The latter unit, which hereafter will be designated as the merchantable type or stand, contained 1,740 trees, 57 percent of which were spruce, 24 percent white pine, and 19 percent hardwoods. Only 673 of these trees were over 6 inches in diameter at breast height in 1930, 52 percent being white pine, 37 percent spruce, and 11 percent hardwoods. Except for a few trees in spots where the drainage is poor, the white pines in both types are vigorous, well foliated, and rapid-growing when not infected with blister rust. As this paper is primarily concerned with blister rust damage to the white pines, discussion of the spruce and hardwoods in the merchantable type will be limited to those facts that are essential in presenting an adequate description of general forest conditions on the area.

Including 66 trees with breast-high diameters of 6 inches or less, the merchantable stand contained 416 white pines, 69 percent of which ranged from 51 to 80 feet in height and the remainder from 21 to 50 feet. Natural pruning had killed the branches on the lower two thirds of the boles. The white pines were distributed throughout the stand, the greatest concentration being on two ¼-acre sample plots where 27 percent of the total number occurred on 21 percent of the area. The merchantable stand is bounded partly by the pasture type, but chiefly by a dense mixed growth of medium-aged conifers and hardwoods (fig. 1).

In 1924 individual plants of the wedgeleaf gooseberry (*Grossularia hirtella* (Michx., Spach) were found generally distributed in the many swampy depressions throughout the pasture type. These bushes had on the average a total of only 54 feet of live stem[6] per acre and were partly concealed in the long grass. Three small skunk currants (*Ribes glandulosum* Grauer), totaling 15 feet of live stem, were also found in the pasture type. Two patches of skunk currants, containing a total of 2,300 feet of live stem and well screened by spruce and hardwood, were situated near the northwestern portion of the merchantable stand. No wild ribes were located in this stand, but small scattered bushes occurred nearby in the pasture and on rock outcrops in the adjoining mixed growth of conifers and hardwoods. The wild ribes were eradicated in 1925. A patch of cultivated black currants, probably *R. nigrum*, was grown on an adjoining farm for several years in an open situation about 800 feet west of the area studied. This currant garden was started about 1909 by a former resident, with a dozen plants imported from a nearby State. The planting was increased by propagation from cuttings until it contained about 80 large bushes, which were destroyed in 1917 by the present tenant, because he was unable to find a suitable market for the fruit. No other cultivated ribes were found, or are known to have existed, within 1 mile of the area.

FIELD METHODS

The data on blister rust damage in the area studied were obtained separately for the two types, because of the difference in character of growth resulting from the difference in stocking. The pasture

[6] Figures for "live stem" represent the total linear measure of stem wood in living canes, branches, and spurs of the plant.

type was divided into twenty-five 1-acre plots, whereas the merchantable stand was studied as a unit. A careful search was made for ribes, and the location, species, and live-stem length were recorded. Detailed information was secured on all white pines, except seedlings less than 4 years old and trees dead from causes other than blister rust, principally suppression and cattle injury. The data obtained for each white pine included location, height, diameter at breast height, age, dominance, and condition of health as influenced by the blister rust. The heights were determined by ocular estimates, checked occasionally by actual tape measurements. Tree diameters were obtained with calipers, and tree ages by counting the yearly growth nodes. In taking the data on dominance, the trees were arbitrarily classified as suppressed or not suppressed, the latter classification including the three normal classes, namely, intermediate, codominant, and dominant. This grouping was chosen in order that trees of little or no value to the stand and those still important might be considered separately. The condition of health as influenced by blister rust was ascertained by climbing the trees and carefully examining them. Each tree was recorded as healthy or diseased. In the case of infected trees it was noted whether or not the disease had reached the trunk.

As long as the pine bark adjoining the canker or area directly affected by the disease remains alive, the blister-rust fungus continues to grow. Thus, cankers on branches frequently continue to extend until the trunk has been reached. The bark invaded by the disease eventually dies as the result of this parasitism. Soon after the canker has encircled the trunk, the diseased bark dies, girdling the tree and causing the death of that portion of the crown above the girdle. The fungus continues its downward growth until it reaches and girdles that section of the trunk below which there is no vigorous supporting foliage, thus killing the entire tree. In this study, white pines with infected trunks were further classified, on the basis of degree of decadence resulting from the disease, under three heads, namely, "top of crown alive", "top of crown dead", and "tree dead".

For the pasture type, the approximate age of the oldest infection was determined on each diseased pine, as there is no method of ascertaining exactly the year during which an infection originated. Since infection takes place through the needles (*1*), it is necessary to determine, from the number of annual nodes, the years during which the diseased portion of the tree bore needles. In this study the year of the infection was assumed to be the same as the year during which the infected internode was formed and first bore needles. Thus, the canker ages recorded are the maximum ages. In northern white pine the needles are normally retained during the second and sometimes the third year; therefore the actual age of an infection may be a year or two less than the recorded maximum.

DEVELOPMENT OF PINE INFECTION ON THE AREA STUDIED

The oldest cankers found on the area resulted from infections on internodes formed in 1908. These infections, however, may have occurred in 1909 or 1910 on needles originating [7] in 1908. As several of the diseased trees in the pasture type were dead, the age of

[7] RICHARDS, J. L. SUSCEPTIBILITY OF DIFFERENT AGED PINE NEEDLES TO BLISTER RUST AND RELATION BETWEEN THE NUMBER OF INFECTIONS ON PINES AND THE PERSISTENCE OF THEIR NEEDLES. U.S. Dept. Agr., Bur. Plant Indus. Blister Rust News 11: 241–247. [Mimeographed.]

the cankers that killed them could not be determined. Therefore, it is possible that the infections on 1908 internodes were not the earliest on the area. However, the disease was undoubtedly established there sometime between 1901, when it was first introduced into northern Vermont, and 1910. If the cankers on 1908 internodes were the first infection, the cultivated black currants planted about 1909 may have been responsible for establishing the blister rust in this locality (*3*).

Of the 2,226 pines on the entire area, 864 (39 percent) were found to be infected with blister rust (table 1). This represents conditions existing on the area when the studies were made, but undoubtedly many small pines had already been killed by the disease and had disappeared. This destruction of young trees is one of the most serious aspects of the damage caused by blister rust, and one of the most difficult to evaluate.

TABLE 1.—*Relation of infection of white pines to length of period of exposure and the average height of the trees during this period*

[Data are as of 1924 for the pasture type and 1925 for the merchantable stand]

Pines originating—	Average height of pines[a]	Minimum years of exposure to possible infection from—		Pines		
		Cultivated black currants	Wild ribes[b]	Total	Infected	
	Inches	*Number*	*Number*	*Number*	*Number*	*Percent*
Before 1910		7	13+	1,210	748	62
1910–12	30.71	5–7	11–13	93	31	33
1913–15	14.40	2–4	8–10	312	53	17
1916–18	7.55	0–1	5–7	545	32	6
1919–21	2.65	0	2–4	66	0	0
Total				2,226	864	39

[a] Average heights of trees during period of exposure to infection from wild ribes were computed from tables by Spring (*11*).

[b] While the actual period of exposure to infection from wild ribes probably extended from 1910 to 1924, inclusive, the years 1923 and 1924 are not considered in these data, because infections occurring in these years were not sufficiently developed to be found in 1924 when the pasture type was studied.

The percentage of pines infected becomes greater with the increase in tree heights and in the number of years of exposure to infection (table 1). The quantity of pine foliage exposed to infection is an important factor influencing the amount of infection. On the basis of foliage volume alone, a large tree has a much greater chance of becoming infected than a small one. Height of tree is an imperfect index of the foliage volume, because among young trees the amount of foliage increases at a much greater rate than the height. However, since no published data are available on the rate of increase of foliage volume with age, the average heights are used in this case to indicate the trend of foliage volume. The fact that no infection was found on the 66 trees originating after 1918 may be the result of their small size or of the removal of the cultivated black currants in 1917.

There were three possible ribes sources for the infection on the area studied: The cultivated black currants that were grown for 7 years northwest of the area; the skunk currant patches located in

1924 just outside the northwest corner of the merchantable type; and the individual bushes, largely wedge-leaf gooseberries, found scattered through the pasture type, likewise in 1924. The ribes record is incomplete, as no definite information is available on the extent or distribution of the population of the two wild species during the infection period under consideration, namely, 1910 to 1922,

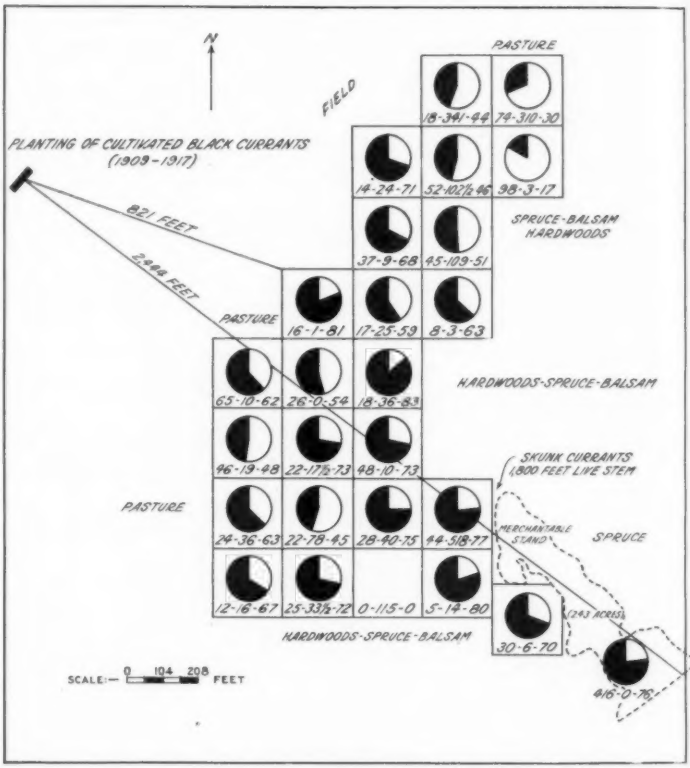


FIGURE 2.—Amount and distribution of pines, ribes, and pine infections on the study area at Waterford, Vt. Only the 1,210 pines are included which originated before 1910 and were therefore exposed to the maximum period of infection. Each square represents a 1-acre plot in the pasture pine type. Broken line indicates boundary of merchantable pine stand. Reading from left to right, numbers separated by dashes in squares indicate, respectively: (1) Number of pines, (2) number of feet of ribes live stem, (3) percentage of pines infected. Shaded portion of each circle illustrates percentage of pines infected in respective plot.

inclusive. Several other factors, aside from the quantity and location of ribes, have undoubtedly influenced the distribution of pine infection among the individual units of the area shown in figure 2, especially the variation in foliage volume and screening of the pines and in topography. Independent of all other factors, in the ten 1-acre plots comprising the four northernmost tiers of those studied, the percentages of pines infected decrease as the distances from the cultivated black currant planting increase. This condition strongly indicates the importance of the ribes (probably cultivated black

currants) northwest of the area as the principal source of the disease in the northern portion. The inverse relationship of the amount of infection and the distance from ribes has been noted on other tracts (7). In the remainder of the Waterford area the influence of the cultivated currants is not clearly indicated by the variation of intensity of infection with distance. It seems probable that the wild ribes contributed materially to the infection found in the southern portion, especially in the vicinity of the skunk currant patches.

BLISTER RUST DAMAGE IN THE MERCHANTABLE STAND

The size of the white pines in the merchantable stand (fig. 3) prevented rapid disintegration of the trees killed by the blister rust and afforded an opportunity to obtain data on the progress of the disease. Moreover, there has been no individual variation in the period of exposure to infection among the trees in this stand. Of course there have been unmeasured changes in the heights, diameters, and crowns of the pines during this period. These variations are necessarily disregarded in the discussion.

The merchantable stand contained 416 white pines, of which 364 (88 percent) were classed as not suppressed (table 2). In 1925, 76 percent of the total pines were infected, 78 percent of the unsuppressed trees and 65 percent of the suppressed trees being diseased. The 1930 examination showed no change in these percentages, since no trees were found to have been initially infected during the period from 1925 to 1930. Especially noteworthy is the higher infection ratio among the pines not suppressed, the best trees in the stand. Undoubtedly, the smaller crowns of the suppressed pines reduced their chances of becoming diseased.

TABLE 2.—*Dominance and blister rust infection of white pines in merchantable stand in 1925 and 1930*

Condition of health as affected by blister rust	Not suppressed				Suppressed				Total			
	Number		Percent		Number		Percent		Number		Percent	
	1925	1930	1925	1930	1925	1930	1925	1930	1925	1930	1925	1930
Trees not diseased	80	80	22	22	18	18	35	35	98	98	24	24
Trees with branch cankers only	76	45	21	12	2	2	4	4	78	47	19	11
Trees with stem cankers:												
Top of crown alive	152	123	42	34	10	3	19	6	162	126	39	30
Top of crown dead	32	43	9	12	10	4	19	7	42	47	10	11
Trees dead	24	73	6	20	12	25	23	48	36	98	8	24
Total	364	364	100	100	52	52	100	100	416	416	100	100

In 1930 only branch cankers were found on 47 white pines, or 11 percent of the total number, regardless of dominance. From the viewpoint of potential damage, the trees in this group may be regarded as ill, with a chance to recover. Pines are sometimes killed by severe pruning caused by numerous branch infections. This type of damage is, however, relatively infrequent in *Pinus strobus*, and it does not occur in the merchantable stand at Waterford. In this area the death of the trees results from cankers that girdle the trunks.

Since the blister rust fungus is wholly parasitic, a canker originating on a branch can reach the trunk only as long as living bark intervenes. The death of the branch, either as a result of natural pruning or of

FIGURE 3.—Dominant, codominant, and intermediate white pines infected with blister rust in a merchantable stand at Waterford, Vt. Eleven pines, marked with white bands, have trunk cankers; two pines, marked with crosses (X), have only branch cankers. Photograph by E. C. Filler, 1926.

girdling by the canker itself, may cause the death of the bark between the canker and the trunk and thereby isolate the canker and kill it by starvation. However, a tree frequently has several branch cankers,

and usually one or more of them will reach the trunk. The progress of the disease in this respect is indicated by the fact that in 31 trees (40 percent of the 78 pines that had branch infections only in 1925) the cankers had reached the trunk by 1930 (table 2).

In 1930 trunk cankers were found on 271 white pines (65 percent of the total number). A trunk canker is almost invariably fatal to the tree, the only known exceptions occurring in the upper part of long terminal shoots that on rare occasions die before the fungus has had time to reach the node below. In the stand under discussion all the trunk cankers were located below the terminal shoot and may be considered fatal to the trees. Of the 271 trees with trunk cankers in 1930, 98, or 36 percent, had already been killed. It is only a question of time as to when the remaining 173 will die as a result of the disease. The rate of killing is indicated by the increase in the number of dead trees, from 36 in 1925 to 98 in 1930 (table 2).

The average annual progress of the disease in damaging this stand between 1925 and 1930 is shown in table 3 in percentages of the total number of infected trees. The rate at which these changes occur is by no means constant but increases or decreases, or even reverses its direction, with the increase in the time elapsing since the date of infection.

RELATION OF TREE SIZE TO AMOUNT OF INFECTION AND RATE OF KILLING

Infection may take place through needles borne on the trunks (*9, p. 28*) and is usually confined to that part of the terminal shoot bearing needles at the time of exposure. Occasionally, infection occurs through adventitious shoots on the trunk. However, trunk cankers usually result from the growth of the fungus into the trunk from points of infection on branches; this was the case in the merchantable stand at Waterford.

The time required by the fungus to reach the trunk through a branch is governed by its distance from the trunk and its rate of growth. Although pines with large crowns and many needles have a greater chance of becoming infected than do small ones, the average distance between the needles and the trunk is greater in large crowns than in small ones. Therefore, the fungus as a rule requires more time to reach the trunk in trees with the larger crowns. Rhoads (*8*) measured the development of cankers on trunks up to 4 inches in diameter and found that the rate of growth of the fungus increased with the diameter of the diseased part. Computations from Rhoads' tabulations show, nevertheless, that despite the increased rate the fungus required more than three times as long to completely girdle a stem in his largest-diameter class than in his smallest because of the disproportionate increase in circumference. This may partly account for the fact that 73 percent of the infected suppressed trees in the merchantable stand had died from blister rust by 1930, whereas only 26 percent of the diseased unsuppressed pines had been killed (table 3).

The status of the health of the pines in the merchantable stand in 1930, as influenced by the blister rust, is shown in figure 4, in which the data are arranged according to the height and diameter of the trees within each of the dominance groups. In considering this figure, it should be noted that the percentages of pines infected, represented by the solid-black column, are now fixed, since further infection of the

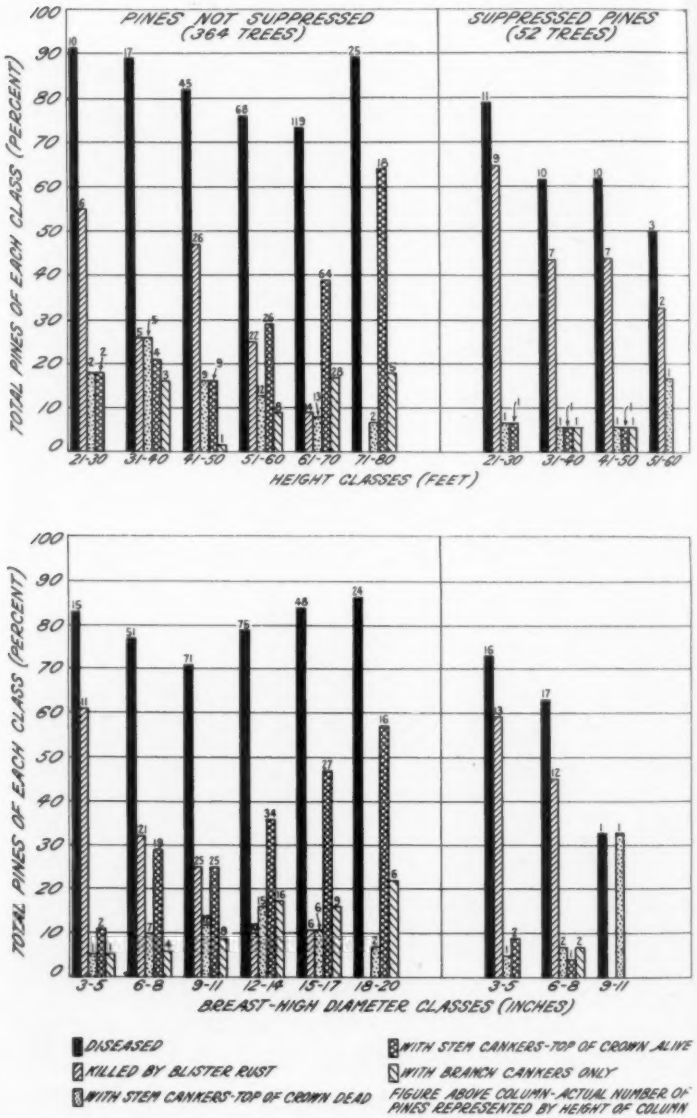


FIGURE 4.—Status in 1930 of health of white pines in merchantable stand as influenced by blister rust. Data arranged according to height and diameter of trees within each dominance group.

trees is being prevented by eradication of the ribes. All other columns, representing percentages of trees in the various damage classes as of 1930, are at temporary levels, which vary as the disease progresses. Unsuppressed pines of all sizes have been attacked by the rust (fig. 5), the number of trees infected ranging from 71 to 91 percent (fig. 4). Moreover, unsuppressed pines of all sizes, except the largest in each class, have been killed. (Forty-nine percent of the 73 dead

TABLE 3.—*Changes in percentages of infected white pines in merchantable stand between 1925 and 1930*

Condition of health as affected by blister rust	Not suppressed			Suppressed			Total		
	1925	1930	Average annual change	1925	1930	Average annual change	1925	1930	Average annual change
	Per cent	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*
Trees with branch cankers only	27	16	−2.2	6	6	0	25	15	−2.0
Trees with stem cankers:									
Top of crown alive	54	43	−2.2	29	9	−4.0	51	39	−2.4
Top of crown dead	11	15	+.8	29	12	−3.4	13	15	+.4
Trees dead	8	26	+3.6	36	73	+7.4	11	31	+4.0

pines in the unsuppressed group were in height classes of 51 to 80 feet, and 56 percent were in diameter classes of 9 to 17 inches (fig. 4).

Since the time required for cankers to reach the trunk and kill the tree is influenced both directly and indirectly by the size of the crown

FIGURE 5.—White pines of all sizes infected and killed by blister rust in northwestern section of merchantable stand at Waterford, Vt. Degree of infection indicated by white markings as follows: 1 band, trunk canker (tree alive in 1930); 2 bands, killed by blister rust (tree alive in 1925, dead in 1930); 3 bands, killed by blister rust (tree dead in 1925); cross (×), branch cankers only, 1925 and 1930; cross and band, branch cankers only in 1925, trunk canker in 1930. Photograph by E. C. Filler, 1930.

and the upper portion of the trunk, both of which are closely related to the diameter of the tree at breast height, some correlation may be expected between diameter and the time required by the disease to kill the tree. When the effect of the disease is measured before the damage is completed, this correlation will be manifested by a downward trend in the proportion of trees killed as the diameter increases. This is the case in the merchantable stand at Waterford as of 1930, the proportion of trees killed by the disease decreasing as the diameter increases. It is evident that when the end of the damage has been reached, blister rust will have killed a majority of the pines in each of the diameter classes.

EFFECT OF BLISTER RUST ON BASAL AREA[5] OF STAND

In 1930 the basal area of the white pines in the merchantable stand, including both the living trees and those killed by the disease, was 306 square feet (table 4), and of the hardwoods and spruce 236 square feet. The total basal area of 542 feet (223 feet per acre) is about normal for a fully stocked stand of this age and composition. Since the suppressed pines had a basal area of less than 10 square feet in 1930 (only 3 percent of the basal area of all the pines), they will not be considered separately in this connection.

TABLE 4.—*Basal area of white pines in the merchantable stand as of 1925 and 1930 as affected by the blister rust*

Condition of health as affected by blister rust	Basal area of white pines (square feet)		Percentage of basal area		Percentage of basal area of all species (1930)[a]
	1925	1930	1925	1930	
Trees not diseased	52	65	20	21	12
Trees with branch cankers only	54	45	21	15	8
Trees with stem cankers:					
Top of crown alive	126	120	48	39	22
Top of crown dead	16	36	6	12	7
Trees dead	12	40	5	13	7
Total	260	306	100	100	56

[a] No basal area or volume data were obtained in 1925 for species other than white pine.

The proportion of the basal area of the white pines represented by trees beginning to die (top of crown dead) and those already dead as a result of the rust increased from 11 percent in 1925 to 25 percent in 1930, an average yearly increase of about 3 percent. The white pines in these two groups in 1930 comprised 14 percent of the total basal area of all species in the stand. Classifying as "doomed" all white pines with trunk cankers and as "may die" all white pines with branch cankers only makes it evident that the disease will eventually reduce the basal area of the white pines between 64 and 79 percent and the basal area of all species in the stand between 36 and 44 percent.

[5] The basal area of a tree is the area of a cross section of the stem at stump height inside the bark and is computed according to the formula: $b=\frac{\pi d^2}{4}$, in which b represents basal area and d the diameter of the cross section inside the bark. In this case, the diameter at breast height outside the bark was assumed to correspond with the diameter at stump height inside the bark.

EFFECT OF BLISTER RUST ON BOARD-FOOT VOLUME[1] OF STAND

In 1930 the volume of the white pines in the merchantable stand, including both the living trees and those killed by the disease, was 52,970 board feet, or 21,798 board feet per acre (table 5). The suppressed white pines contained but 1,036 board feet, or less than 2 percent of the total amount for this species. The volume of all other species was 21,644 board feet, or 8,907 board feet per acre, bringing the total contents of the entire stand up to 30,705 board feet per acre. This amount is below normal for a fully stocked mixed stand containing a large proportion of 60-year-old white pines. The difference may be partly due to the indeterminable loss in increment for that period during which each fatally diseased pine has suffered reduced or interrupted growth.

As indicated in table 5, the proportion of total pine volume represented by trees beginning to die (top of crown dead) and those already dead as a consequence of the disease increased from 8 percent in 1925 to 23 percent in 1930, an average increase of 3 percent per year. In 1930 the pines in these two classes contained 16 percent of the total board-foot contents of all species in the stand. The ultimate effect of blister rust will reduce the volume of the white pines between 64 and 80 percent, and the volume of all species in the stand between 46 and 57 percent.

TABLE 5.—*Board-feet volume of white pines in the merchantable stand as of 1925 and 1930, as affected by blister rust*

Condition of health as affected by blister rust	Volume of white pines (board feet)		Percentage of volume		Percentage of volume of all species (1930)
	1925	1930	1925	1930	
Trees not diseased	8,453	10,693	19	20	14
Trees with branch cankers only	9,437	8,209	22	16	11
Trees with stem cankers:					
Top of crown alive	22,160	21,904	51	41	30
Top of crown dead	2,280	6,132	5	12	8
Trees dead	1,518	6,032	3	11	8
Total	43,848	52,970	100	100	71

EFFECT OF BLISTER RUST ON STOCKING OF STAND

The merchantable stand, with 277 trees over 6 inches in diameter per acre, was about fully stocked before blister rust began to take its toll. Of these trees, 50 percent were unsuppressed white pines, 2 percent were suppressed white pines, and 48 percent were trees of other species, largely spruce. Between 239 and 284 of the 364 unsuppressed white pines on the 2.43 acres in the stand will eventually be killed by blister rust (table 2). This will leave between 80 and 125 unsuppressed white pines, or from 33 to 51 per acre. This great reduction in stocking is even more serious than these figures indicate, because of the irregularity of the original stocking.

The two ¼-acre plots (fig. 6, A_1, B_1) are samples of the best pine stocking in the merchantable stand. On this half acre, there were 101 white pines and 38 spruce or hardwoods with breast-high diam-

[1] Volumes for pine, spruce, and hardwoods are based on tables prepared by Lyford and Margolin (*4*), Woolsey (*5, p. 136*), and Dana (*2*), respectively.

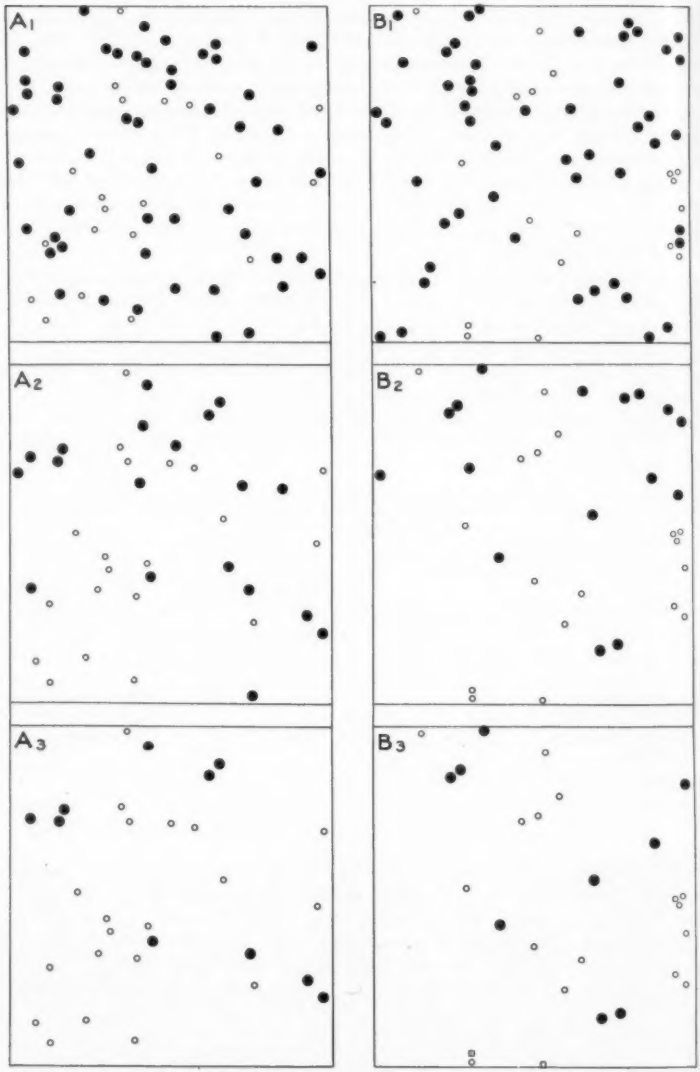


FIGURE 6.—Effect of blister rust in reducing stocking on two ¼-acre plots in merchantable stand: A_1 and B_1, two ¼-acre plots, showing location of trees of all species whose breast-high diameters exceed 6 inches; A_2 and B_2, same as A_1 and B_1, omitting pines sure to die from blister rust; A_3 and B_3, same as A_2 and B_2, omitting also those pines which may die from blister rust. White pines whose breast-high diameter exceeds 6 inches are indicated by solid dots (●); spruce or hardwood whose breast-high diameters exceed 6 inches are indicated by smaller open circle (○).

eters greater than 6 inches. Blister rust will eventually reduce this stocking below that shown in A_2 and B_2 and will produce conditions approaching those shown in A_3 and B_3. In addition to the trees shown in figure 6, the two ¼-acre plots contained many small spruce and 12 suppressed pines with breast-high diameters under 6 inches. Seven of these pines are doomed as a result of trunk cankers, and one other has a branch infection that may eventually cause its death.

EVALUATION OF BLISTER RUST DAMAGE

Up to 1930 the economic loss caused by blister rust in the merchantable stand was relatively small. The pines killed by the disease on the 2.43 acres had a volume of 6,032 board feet (table 5). Blister rust does not injure the wood but may cause a constriction of the trunk in the portion covered by the canker. In the merchantable stand most of the cankers were above the commercial parts of the trees. However, it is doubtful if any of these dead pines could now be salvaged. Such trees deteriorate rapidly as a result of boring insects and wood-rotting fungi. The wood of these dead pines may, therefore, be considered a definite loss, amounting, at a normal stumpage value of $8 per thousand, to $48.26, or $19.86 per acre.

The potential economic loss to this stand by blister rust includes all trees with trunk cankers and those with branch cankers that may die from the disease. The potential loss is, therefore, at least between 34,068 and 42,277 board feet on the 2.43 acres. It may even exceed this maximum figure by the amount of increment made by the diseased trees between 1930 and the time of their death. Moreover, these estimates of potential loss do not include the additional increment that would normally have occurred had the trees remained free of blister rust. Computed at a normal stumpage value of $8 per thousand, the indicated potential loss amounts at least to between $112.16 and $139.18 per acre. This potential loss is the result of infections from ribes that were eradicated 5 to 13 years before the 1930 examination. Had these ribes been allowed to remain, potential loss would in all probability have approached 100 percent for the white pines in the stand.

The economic loss in this stand as a result of the disease may be kept at the present figure by immediately logging the entire stand. This may not, however, be practical, because of the small area and the condition of the lumber industry. Consequently, the loss continues to mount, approaching the highest potential-damage figure.

The economic loss from blister rust on this merchantable stand is far above the average for tracts of white pine of this size and age within the range of this species in the East. However, merchantable trees fatally attacked by the disease can be found in considerable numbers as scattered individuals or small groups throughout the white pine regions of New England and New York. This particular area illustrates the potential destructiveness of the disease to unprotected merchantable stands. Frequently, the damage is not recognized by pine owners until it is too late to utilize the diseased trees. Even in cases where the owners are aware of the increasing damage, the difficulty of detecting infected trees, particularly those with only branch cankers, and the additional cost of making selective cuttings may prohibit the salvage of white pines attacked but not yet killed by blister rust.

SUMMARY

This paper presents data on the occurrence and effect of blister rust on white pine in an area at Waterford, Vt., especially in a stand of merchantable timber.

A patch of cultivated black currants existed for at least 7 years, beginning about 1909, within a few hundred feet of the area. These cultivated bushes appear to have been an important source of infection. Wild ribes also participated in the spread of disease on the area. The cultivated black currants were destroyed in 1917 and the wild ribes in 1925. The earliest infections occurred between 1908 and 1910.

Data on the 2,226 pines on the entire area, grouped according to tree height and number of years of exposure to infection, show that the percentage of pines infected ranged from 0 to 62 percent, the proportion becoming greater with the increase in height and in number of years of exposure to the infection.

The merchantable stand was composed of a mixture of spruce, white pine, and hardwoods, about 60 years old. In 1930, 76 percent of the 416 white pines in this stand were infected, and 65 percent were doomed as a result of trunk cankers. Twenty-four percent of the total pines had already been killed. The percentage of diseased pines killed increased from 11 percent in 1925 to 31 percent in 1930, an average yearly increase of 4 percent.

The proportion of infected trees was greater in the unsuppressed group than in the suppressed group, probably because of the larger individual crowns in the former class. However, partly, at least, because of their smaller size, the suppressed pines were being killed more quickly than those not suppressed.

Pines of all height and diameter classes represented had been attacked by the rust, and in each class, except the largest-size group, some of the trees had already been killed.

The proportion of the basal area of the white pines represented by trees beginning to die or already killed by the rust increased from 11 percent in 1925 to 25 percent in 1930, an average yearly increase of about 3 percent. The killing of trees by the disease will eventually reduce the basal area of the white pines between 64 and 79 percent and the basal area of all species between 36 and 44 percent.

The proportion of the total board-foot volume of the white pines represented by trees beginning to die or already dead from the disease increased from 8 percent in 1925 to 23 percent in 1930, an average yearly increase of 3 percent. Ultimately, the volume of the white pines will be reduced between 64 and 80 percent and the volume of all species between 46 and 57 percent as a result of the disease. Had not the further spread of infection been stopped by the removal of the ribes 5 to 13 years before the 1930 examination, the ultimate loss of white pines would have approached 100 percent.

When damage from the disease has reached its maximum an average of between 33 and 51 unsuppressed white pines per acre will remain. This pronounced reduction in stocking is rendered still more serious by the unevenness of the original stocking.

The actual economic loss in the merchantable stand from blister rust, computed at a normal stumpage value of $8 per thousand, amounted to $19.86 per acre in 1930. As additional diseased white

pines die or deteriorate, the loss will increase toward a maximum of at least between $112.16 and $139.18 per acre, depending on the period of delay in logging the stand.

LITERATURE CITED

(1) CLINTON, G. P., and MCCORMICK, F. A.
1919. INFECTION EXPERIMENTS OF PINUS STROBUS WITH CRONARTIUM RIBICOLA. Conn. Agr. Expt. Sta. Bul. 214: [428]–459, illus.

(2) DANA, S. T.
1909. PAPER BIRCH IN THE NORTHEAST. U.S.Dept.Agr., Forest Serv. Circ. 163, 37 p., illus.

(3) DETWILER, S. B.
1928. BLACK CURRANT SPREADS WHITE-PINE BLISTER RUST. U.S. Dept. Agr. Misc. Pub. 27, 8 p., illus.

(4) LYFORD, C. A., and MARGOLIN, L.
1906. FOREST CONDITIONS IN SOUTHERN NEW HAMPSHIRE. N.H. Forestry Comn. Bien. Rpt. 1905–6: 161–276, illus.

(5) MUNNS, E. M., and BROWN, R. M., compilers.
1925. VOLUME TABLES FOR THE IMPORTANT TIMBER TREES OF THE UNITED STATES. PART II, EASTERN CONIFERS. U.S.Dept.Agr., Forest Serv. 146 p.

(6) PIERCE, R. G.
1917. EARLY DISCOVERY OF WHITE PINE BLISTER RUST IN THE UNITED STATES. Phytopathology 7: 224–225.

(7) POSEY, G. B., and FORD, E. R.
1924. SURVEY OF BLISTER RUST INFECTION ON PINES AT KITTERY POINT, MAINE, AND THE EFFECT OF RIBES ERADICATION IN CONTROLLING THE DISEASE. Jour. Agr. Research 28: 1253–1258, illus.

(8) RHOADS, A. S.
1920. STUDIES ON THE RATE OF GROWTH AND BEHAVIOR OF THE BLISTER RUST ON WHITE PINE IN 1918. Phytopathology 10: [513]–527.

(9) SPAULDING, P.
1922. INVESTIGATIONS OF THE WHITE-PINE BLISTER RUST. U.S. Dept. Agr. Bul. 957, 100 p., illus.

(10) ———
1929. WHITE-PINE BLISTER RUST: A COMPARISON OF EUROPEAN WITH NORTH AMERICAN CONDITIONS. U.S. Dept. Agr. Tech. Bul. 87, 59 p., illus.

(11) SPRING, S. N.
1905. THE NATURAL REPLACEMENT OF WHITE PINE ON OLD FIELDS IN NEW ENGLAND. U.S.Dept.Agr., Bur. Forestry Bul. 63, 32 p., illus.

CYTOLOGY AND BREEDING OF RUBUS MACROPETALUS, THE LOGAN, AND RELATED BLACKBERRIES[1]

By GEORGE M. DARROW, *senior pomologist, Division of Fruit and Vegetable Crops and Diseases,* and A. E. LONGLEY, *associate botanist, Division of Genetics and Biophysics, Bureau of Plant Industry, United States Department of Agriculture* [2]

INTRODUCTION

The highest dessert quality among dewberry and blackberry varieties appears to be found in a group derived wholly or in part from *Rubus macropetalus* Dougl. and related species of wild trailing blackberries that occur in the western parts of California, Oregon, Washington, and British Columbia. Among the high-quality varieties in this group are the Logan, Young, and Ideal Wild or Santiam. All are characterized by excellent flavor and a relative absence of seediness as compared with other varieties of blackberry. The flavor is strongest in the Logan and mildest in the Young, and suggests the flavor of the red raspberry more than that of the eastern American or European forms of blackberries that have been studied. Because of the great value of this group in breeding for high-quality varieties, this study of their cytology and relationship was begun.

MATERIALS

This investigation was carried on chiefly at Corvallis, Oreg. There were available for study several hundred seedlings of the Logan; also many Logan × Lucretia, Logan × Young, and Logan × Mammoth crosses made by C. E. Schuster, formerly of the Oregon Agricultural Experiment Station. There were also at the Oregon station the Ideal Wild or Santiam, Mammoth, Cory, Young, and Lucretia varieties, all of which, except the Lucretia, are derived wholly or in part from these western species.

Material of the wild *Rubus macropetalus* was obtained from fence rows near the station and from other places. Material of a cross of *R. macropetalus* × Logan, made by J. W. Ware, was obtained from western Washington. Other reported crosses of *R. macropetalus* × Logan were examined at Ware's ranch in western Washington and near Monroe and Florence, Oreg. Still other crosses of the wild *R. macropetalus* with various bramble varieties have been observed from time to time. The wild forms were studied at many points in

[1] Received for publication Apr. 7, 1933; issued September 1933.

[2] The writers express their appreciation to the workers at the Oregon State Agricultural Experiment Station, Corvallis, Oreg., for many courtesies and assistance in these investigations; also to S. F. Blake, Division of Botany, Bureau of Plant Industry; L. H. Bailey, Ithaca, N. Y.; and W. L. Jepson University of California, for the reading and criticism of the manuscript.

western Washington, Oregon, and California, from sea level to altitudes of about 5,000 feet in the Cascades, and to some extent in British Columbia.

The material for cytological preparations was collected at the experimental plots of the Oregon State College farm and from the wild in several nearby localities and at various points along the coast of California. Buds that had apparently developed to the stage when pollen mother cells were in the meiotic phases were picked and put at once into Carnoy's killing fluid. After a half hour the fluid was poured off and the buds were covered with absolute alcohol. Acetocarmine smear preparations of the pollen mother cells were then made.

PACIFIC COAST SPECIES OF RUBUS

CHARACTERIZATION

The western trailing blackberries differ from eastern species of dewberries and blackberries in being chiefly dioecious, with the staminate flowers usually much larger than the pistillate ones; in having leaves with leaflets—usually 3, often 5 in vigorous plants, but rarely 1—generally pinnate; and in having shoots and canes more or less glaucous. Western forms have 42, 35, 28, and 21 chromosomes, whereas most eastern trailing forms have 21. The western forms have much smaller drupelets and seeds than the eastern trailing species.

The western trailing blackberries are here considered as consisting of 3 species, although 5 or more species have been recognized by systematists. The following have been referred by Rydberg (*10*) [3] to the section *Ursini* of *Rubus:*

Rubus ursinus Cham. and Schlecht., in Linnaea 2: 11. 1827.
R. vitifolius Cham. and Schlecht., in Linnaea 2: 10. 1827.
R. helleri Rydb., ex Brit. and Brown, North Amer. Flora 22: 460. 1913.
R. eastwoodianus Rydb., ex Brit. and Brown, North Amer. Flora 22: 460. 1913.
R. macropetalus Dougl., ex Hook., Fl. Bor. Amer. 1: 178. 1832.

Rydberg separates *Rubus eastwoodianus* and *R. macropetalus* from *R. ursinus* largely because of the glabrous fruit and sparingly pubescent leaves of the first two; and *R. vitifolius* and *R. helleri* from *R. ursinus* because of the sparingly pubescent leaves and stems of *R. vitifolius* and *R. helleri*, although all three species have pubescent fruit.

Bailey (*4*) in his latest monograph describes three species of the wild trailing blackberries of the Pacific region, namely, *Rubus ursinus*, *R. macropetalus*, and *R. eastwoodianus*. *R. ursinus* is described as a nonglandular tomentose or hairy species and *R. macropetalus* and *R. eastwoodianus* as glabrous or glabrescent, *R. macropetalus* being glandular and *R. eastwoodianus* nonglandular. Bailey does not recognize *R. vitifolius*, because it is represented by a description only, with no type specimen, and because he has found no *Rubus* which would answer the original description. Rydberg's description of *R. eastwoodianus* answers the original description of *R. vitifolius* closely, and according to Bailey (*4, p. 305*), it was established on two specimens collected in the region from which *R. vitifolius* was collected and described.

The writers' collections and studies appear to justify the establishment of three species, which include the important forms on the

[3] Reference is made by number (italic) to Literature Cited, p. 330.

Pacific coast. Rare forms may still be found which will necessitate the establishment of additional species, but those examined seemed to represent crosses between overlapping species.

The three Pacific coast species are *Rubus macropetalus* Dougl., *R. ursinus* Cham. and Schlecht., and *R. loganobaccus* Bailey (*2*, *3*). *R. macropetalus* is by far the most abundant, being the only species found throughout western British Columbia, Washington, and Oregon. Its southern range extends into the highlands of California. *R. ursinus* and *R. loganobaccus* are confined chiefly to the lowlands of a narrow belt of the coast of northern and central California.

Rubus macropetalus in Oregon and Washington is distinct from the two California species, having in general thinner, relatively longer, and more deeply serrate leaves. It is less hairy and more glandular than *R. ursinus* and has much slenderer and more trailing canes than *R. loganobaccus*. *R. loganobaccus* is separated from *R. ursinus* and from *R. macropetalus* by its much greater stature and by the larger size of most of its parts.

Rubus loganobaccus was described by Bailey as a species on the basis of the horticultural variety Logan, of which no wild form was known. In the writers' survey, however, closely related forms were found over a north and south range of some 400 miles. They were especially abundant in the region near Eureka, Calif., constituting the only wild forms in some large areas there. Because they are such giant forms as compared with *R. macropetalus* and *R. ursinus*, they clearly represent another species. Where this species comes in contact with *R. macropetalus* north of Eureka, intermediate forms were observed; likewise, forms intermediate between *R. loganobaccus* and *R. ursinus* were collected south of San Francisco, especially near Watsonville. That the wild *R. loganobaccus* originated from natural crosses of the Logan with *R. ursinus* is untenable, because (1) the observed crosses of the Logan with *R. macropetalus* (similar in size to *R. ursinus*) are not giant in stature but are intermediate, (2) the wild forms cover too great an area, and (3) in the herbarium of the University of California is a collection of the giant form (no. 372722 from Sonoma County), which was made in 1881, the year when the seed from which the Logan originated was said to have been planted.

The following description of *Rubus loganobaccus*, based on wild plants, includes its essential specific characteristics.

Rubus loganobaccus Bailey.—Primocanes [4] erect to 2.5 m, then arching and trailing, stout (0.7 to 1.0 cm or more in diameter), usually glaucous, pubescent; prickles many, long, short, or both, straight or curved, rather weak, with enlarged base; leaves evergreen, glabrate to gray tomentose below, unequally serrate, those of primocanes 3- to 5-pinnately foliate on prickly tomentose petioles, leaflets ovate to triangular-ovate, terminal one on a petiolule 2 to 3.5 cm long, sometimes obscurely to prominently lobed, lateral leaflets with very short petiolules (½ cm). Floricanes [5] with 6 to 15 or more flowers on leafy shoots, pedicels sometimes glandless, usually with some glandular hairs, sometimes with many glandular hairs, prickly, tomentose; flowers usually staminate or pistillate; petals of pistillate flowers small to about 1 cm long, those of staminate flowers much longer to about 2 cm long; calyx tomentose, bristly, sometimes prickly; fruit oblong or conical, sweet, usually 1 inch or less long, blackish, glabrous or pilose.

Habitat.—Fields, valleys, and hills of the coast of northern and central California, from about 40 miles north of Eureka south to Carmel, approximately within the redwood area.

[4] First-year shoots.
[5] Second-year bearing canes.

The Logan differs from the wild *Rubus loganobaccus* in its hermaphrodite flowers and red fruit but is not more vigorous.[6] The Logan may be considered a glandless form with leaves gray tomentose below.

Rubus ursinus is here considered the coastal representative of *R. macropetalus* in California, differing from the latter in having the leaves usually thicker, more pubescent, and less sharply and deeply serrate; canes and inflorescence pubescent; few or no glandular hairs on the inflorescence; and fruit usually pilose. To the north and in the mountains *R. ursinus* varies toward *R. macropetalus*; in Oregon and Washington, forms of *R. macropetalus* vary toward *R. ursinus*. Typically, however, the two species are quite distinct. At Carmel a form was collected that probably should be considered a variety (*monophyllus*)[7] of this species, having most of the leaves entirely or slightly lobed. Throughout the coast region north and south of San Francisco may be found forms that differ from the type in one or more characteristics. Some are glabrate, others glandular, and others slightly to deeply and unequally serrate.

Rubus macropetalus is relatively distinct except as it varies toward *R. ursinus* and *R. loganobaccus* in western California. It is essentially a glabrous, deeply serrate thin-leafed form having slender glaucous canes with glandular hairy inflorescences. Eastward in Idaho and southward in central and southern California it varies considerably in leaf characters from this type. In any one region, moreover, it remains a variable form.

In western Oregon and Washington, and in California in the same locality, may be found forms of *Rubus macropetalus* ranging from pubescent to nearly glabrous and having canes ranging from stout to slender, prickles ranging from few to many, and leaves ranging from pubescent to nearly glabrous and from pointed to obtuse. The inflorescence ranges in hairiness from slightly glandular to quite glandular, occasionally very glandular, and in size of clusters from large to small. The berries range from long to short, from rather firm to soft, and are usually purplish black but occasionally red or white.

On Bainbridge Island, Wash., a nearly thornless plant was seen, and at Puyallup, Wash., a completely thornless one. Shade forms have fewer thorns than those growing in open fields. The shape of leaves on the same plant may vary greatly according to whether the cane grew in early or in late summer. The early summer forms have much longer, more pointed leaves; the later canes, less serrate, shorter leaves. The leaves persist until midwinter and often throughout the winter, especially in protected places.

Near the summit of the Coast Range near Triangle Lake, Oreg., several hermaphrodite plants were found. One plant there produces male flowers in the spring but is hermaphrodite when flowering in the fall. Though normally having dark wine-purple fruit, forms with large red fruit have been selected for cultivation. Forms are reported that produce berries as large as the Logan.

This species is found chiefly in open woods, fields, and along roadsides. The finest berries are produced by bushes growing in moist,

[6] George F. Waldo in a letter dated July 6, 1933, states that he found wild hermaphrodite plants of *Rubus loganobaccus* near Eureka, Calif.

[7] *Rubus ursinus monophyllus*, var. nov. Folia maxima ex parti integra vel leviter trilobata interdum trifoliolata. Carmel, Calif., May 8, 1932; G. M. Darrow. Type in U.S. National Herbarium, no. 1566198.

partially shaded locations. Where forest fires are not too severe, the tangled cane growth often comprises the principal part of the vegetation of cut-over land for a few years, until the undergrowth and trees become large enough to kill it with excessive shade. In favorable seasons it bears fruit of fair size in great abundance. East of the Cascade Mountains and south in California it is found chiefly in the moist ravines. As it flowers very early in the spring, frosts and rains are considered to be responsible for the small size and the poor set of the fruit in some years. In an open field or by the roadside (fig. 1) the mature plants of this species are hardly 2 to 3 feet high, but where they climb over brush or stumps their canes may be many feet in height.

CHROMOSOME STUDIES

Chromosome material was secured from male plants of the dioecious form of *Rubus macropetalus*, common in the wild, and from the perfect-flowered cultivated form known as the Ideal Wild variety.

In material collected from four distinctly separate localities in Oregon, the haploid chromosome number of male plants of the

FIGURE 1.—Wild *Rubus macropetalus*, showing trailing habit.

dioecious form of *Rubus macropetalus*, common in the wild, was found to be 42. This number is the highest that has yet been reported for a *Rubus* species and it seems significant that this high number is associated with dioeciousness.

Figure 2, C, shows a heterotypic metaphase from material collected 10 miles from Corvallis, Oreg., on the Newport road. Figure 2, B, shows a homotypic metaphase from material collected on the summit of the highway 40 miles south of Roseburg, Oreg. The figures in this wild material were frequently very clear, and the regular behavior of the chromosomes made accurate counting possible in spite of the large number.

The haploid chromosome number of male plants of *Rubus loganobaccus* collected from the wild in two widely separated localities was 21. One of these localities, about 42 miles north of Eureka, Calif., was the northernmost point at which this species was found. The other locality, where two collections were made, was Aptos, Calif., about 350 miles southward. Plants collected from a third locality, Scotia, Calif., nearly 30 miles south of Eureka, had 35 chromosomes.

In a fourth collection, at Carmel, Calif., the most southern station for this species, the plants had 28 chromosomes. Material of a form closely resembling *R. macropetalus* and collected near the *R. loganobaccus* plants at the northernmost station, 42 miles north of Eureka, also had 28 chromosomes. It seems probable that the chromosome number of *R. loganobaccus* is 21.

The haploid chromosome number of the Ideal Wild variety is 28. Figure 2, A, shows a typical heterotypic metaphase of this form. The 28 chromosomes can be counted in the early meiotic phases, since univalent chromosomes were rarely seen. This variety originated

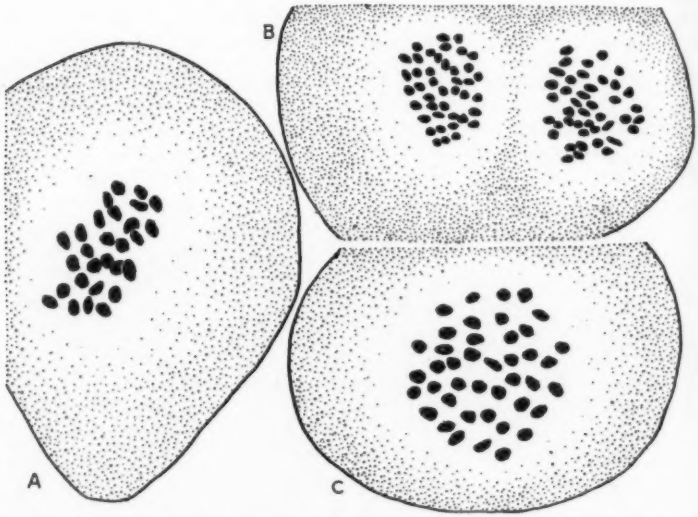


FIGURE 2.—Chromosomes in *Rubus macropetalus* and related form: A, Heterotypic metaphase in the perfect-flowered form, Ideal Wild; B and C, homotypic and heterotypic metaphase, respectively, in *R. macropetalus* from the wild.

in a garden in Salem, Oreg., and although it resembles *Rubus macropetalus*, its hermaphrodite flowers and somewhat tomentose leaves suggest that it originated from a *R. macropetalus* × Logan hybrid.

THE LOGAN

HISTORY

Kinney (*8*), Darrow (*7*), Backhouse (*1*), and others have discussed the origin of the Logan. According to reports by the originator, J. H. Logan, of Santa Cruz, Calif., in 1881 he planted seed of the Aughinbaugh, an extremely vigorous pistillate selection of the wild *Rubus*, but having larger, darker leaves, and fruit similar to the Logan in shape. This plant grew in Logan's garden near the Texas Early blackberry and a red raspberry similar to the Red Antwerp. The resultant seedlings, with one exception, were said to be similar in appearance. The exceptional plant later was named the Loganberry. The majority of the seedlings were considered crosses of the Aughinbaugh and the Texas Early blackberries. The Mammoth blackberry

was selected either from this first lot or from later ones and was similar to the majority of the seedlings. Seedlings other than the Logan and the Mammoth were distributed but were said to be pistillate and were later discarded. The Logan was perfect-flowered and red-fruited and was considered a cross of the Aughinbaugh blackberry and the Red Antwerp raspberry. Logan stated that seedlings of the Logan which he later raised were similar to it, having red, mostly small fruit, and that some hundreds of crosses of the wild blackberry with the Logan, Mammoth, and Black Logan were perfect-flowered but sterile.

In 1916 Backhouse (*1*) questioned the hybrid origin of the Logan because it did not show segregation but resembled in breeding behavior a variety of a true species.

Crane and Darlington (*5*) studied the cytology and inheritance of the Logan. They found that it had 21 chromosomes. Selfed seedlings showed segregation of characters for glaucous and nonglaucous shoots in a 3 to 1 ratio. Other characters were not sufficiently distinct to determine ratios. These workers also studied the Laxton berry, a cross of the Superlative (a red raspberry) × Logan, and a sister plant. Each had 49/2 chromosomes and showed segregation of characters in the seedlings. They concluded that the Logan was of hybrid origin, that it may have originated from an octoploid (28) blackberry crossed with a tetraploid (14) raspberry, and that because of the greater proportion of blackberry chromosomes, the raspberry characters were largely lost. They further stated that such a form would fail to segregate the characters of the parents because the pairing of the chromosomes of the two parents would lead to irregularities in division and to the segregation of entirely new types whose vitality would usually be reduced. They stated that this actually occurs in the Logan, "such a large proportion of whose offspring can only be described as defective."

BREEDING AND CYTOLOGY

Logan Selfed

The several hundred selfed seedlings of the Logan which have fruited at the Oregon Agricultural Experiment Station showed the variations that might be expected among seedlings of a variety of a true species. Nearly all seemed about as vigorous as the Logan and many were much more vigorous. However, a large number of dwarfs were destroyed because they resembled plants affected with the "dwarf" virus disease. The various seedlings ripened from a week earlier to approximately 2 weeks later than the Logan; several bore larger fruit, but nearly all bore smaller fruit; some were better flavored than the Logan, but many were more acid; less than 1 percent bore fruit having the calyx attached when picked; none separated from the receptacle as in the raspberry; less than 1 percent bore glabrous fruit; none of the several hundred were entirely sterile, most being very productive. In cane, leaf, and fruit there was no suggestion of the raspberry. Of more than 400 seedlings, all or nearly all, were productive and were not defective as reported by Crane and Darlington (*5*).

Table 1 shows data on the fruit and seed of the Logan as compared with those of Logan seedlings and other varieties. The measurements were made on 10 berries of each variety. The seed of the Logan is shown to be much larger than that of the Cuthbert red raspberry or that of *Rubus macropetalus*.

TABLE 1.—*Fruit and seed of the Logan as compared with those of Logan seedlings, four other blackberry varieties, and the Cuthbert red raspberry*

[Data represent averages of measurements on 10 berries]

Variety	Weight of berry	Drupelets per berry	Seed weight
	Grams	*Number*	*Milligrams*
Logan	7.22	98.6	2.55
Logan seedlings	2.38–5.72	58.1–96.6	1.80–2.99
Rubus macropetalus	----------	54.9	1.39
Ideal Wild	2.30	44.6	1.67
Young	8.34	73.8	3.82
Mammoth	5.88	96.0	2.32
Cuthbert red raspberry	2.80	85.2	1.43

It is worthy of note that several variations have been observed in fields of Logan blackberries in Oregon. In some cases the variant plants came into leaf earlier than the rest; in others, the canes were less glaucous. Their appearance suggested that they had originated

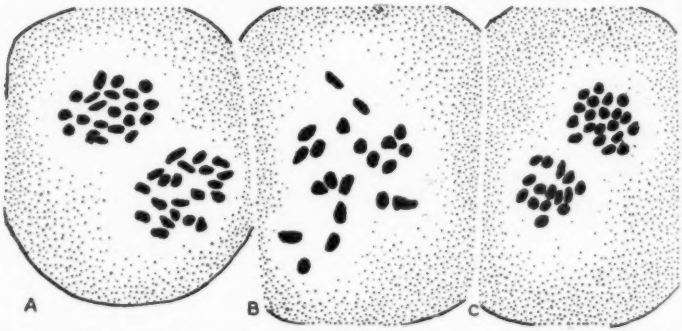


FIGURE 3.—Chromosomes in the Logan and in selfed Logan seedlings: A, Homotypic metaphase in the Logan; B, prophase in a hexaploid Logan seedling (no. 14); C, homotypic metaphase in a pentaploid Logan seedling (no. 3).

as seedlings of the Logan but bearing similar fruit. One Logan plant had produced some thornless (but fruitless) canes that were obviously bud sports.

The fruit clusters of the Logan were compared with those of its seedlings. Forty-eight clusters of the Logan had an average of 7.9 berries, whereas averages of 10 clusters each of 30 seedlings ranged from 3.7 to 10 and averaged 6 berries. Of 409 seedlings 269 had glaucous and 140 glabrous canes, approximating a 2 to 1 ratio. Crane and Darlington (*5*) listed 40 seedlings having waxy canes and 13 devoid of wax, which suggested a 3 to 1 ratio.

The haploid chromosome number of the Logan is 21. This number for a clonal offspring of the original plant agrees with that given by Crane and Darlington for seedling offspring. The chromosomes of the Logan were generally found to pair regularly, and the reduction phases show only occasional irregularities in chromosome distribution. Figure 3, A, is a typical homotypic metaphase in which 21 chromosomes are shown on each plate.

The chromosomes of 11 seedlings of the Logan, selected at random, were examined; 10 of these had the same chromosome number as that of the parent plant. Figure 3, B, shows a prophase stage from plant 14. At this phase the chromosomes frequently show variations in size and shape, but are small and do not lend themselves to a detailed morphological comparison. The chromosome behavior during meioses of the pollen mother cells in the 10 hexaploid seedlings is generally as regular as that found in the mother plant. Occasionally preparations from a few of the plants showed unpaired chromosomes at diakinesis and random distribution of these univalents if they did not divide in the heterotypic division. If they divided, the halves went at random to the poles in the homotypic division.

The eleventh plant (no. 3 in table 2) of this small group of seedlings was found to be pentaploid. The chromosome behavior of the plant is distinctly more irregular than that found in any of the 10 sister plants. There were always some unpaired chromosomes in the prophase of the heterotypic division, and irregularities in chromosome distribution were prevalent in both divisions. Occasionally, chromosomes were extruded into the cytoplasm during the heterotypic division. Figure 3, C, shows a homotypic metaphase with 15 chromosomes on one plate and 20 on the other. Figures at this phase frequently show such unequal numbers; in some cells there are minor spindles around chromosomes previously extruded into the cytoplasm.

Table 2 shows the character of the pollen in the plants used in this study. The hexaploid Logan seedlings have a low percentage of sterile pollen. The pentaploid plant has approximately 50 percent of its pollen grains aborted.

TABLE 2.—*Chromosome number and pollen counts in the Logan variety, Logan seedlings, hybrids, and related forms*

Variety or species	Seedling no.	Number of chromosomes	Number of pollen grains in condition indicated	
			Good	Poor
Logan		21	133	5
Logan seedling	3	35/2	111	90
	4	21	480	180
	5	21	135	38
	7	21	104	11
	8	21	140	11
	10	21	152	21
	11	21	110	4
	12	21	105	10
	13	21	114	18
	14	21	133	15
	16	21	118	14
Mammoth		21	239	98
Logan × Mammoth	4	35/2	0	100
	5	21	117	8
	6	21	44	100
	7	35/2	(a)	(b)
	8	21	127	18
	10	21	132	12
	12	21	203	7
	13	21	56	314
Young		21		

[a] Less than 10 percent. [b] More than 90 percent.

TABLE 2.—*Chromosome number and pollen counts in the Logan variety, Logan seedlings, hybrids, and related forms*—Continued

Variety or Species	Seedling no.	Number of chromosomes	Number of pollen grains in condition indicated	
			Good	Poor
Logan × Young	1	21	[a]	[b]
	2	21	128	21
	3	21	112	168
	4	21	122	38
	5	21	127	37
	6	21	146	77
	6A	21	122	72
	7	21/2	9	114
	8	21	130	12
	9	21	151	25
Lucretia		21		
Logan × Lucretia	1	21	100	80
	2	21	108	78
	3	21	104	31
	4	21	139	103
	5	21	100	106
	6	21	104	36
	8	21	124	16
	12	21	120	90
	13	21	108	213
Phenomenal		21		
Cory		21		
Rubus macropetalus		42	126	2
Ideal Wild		28	106	19

[a] Less than 10 percent. [b] More than 90 percent.

Earlier studies of *Rubus* (*9*) showed that forms with an even multiple of the basic chromosome number 7 are much more fertile than those with an odd multiple. Crane and Lawrence (*6*) in their study of *Rubus* have confirmed this relationship between the chromosome number and the fertility of the pollen.

The results of the pollen study of the few representative Logan seedlings are in agreement with these earlier studies, the pentaploid being the only plant showing a high percentage of sterile pollen.

LOGAN × MAMMOTH HYBRIDS

The Mammoth originated about the same time as the Logan but was considered a hybrid between Aughinbaugh, a variety of *Rubus ursinus*, and Texas Early blackberry (close to *R. argutus* Link × *R. enslenii* Tratt.). It is an even more vigorous plant than the Logan. Its canes and thorns are much larger and suggest to some extent the eastern blackberry. Its pollen showed a relatively high percentage of sterile grains (29 percent as compared with 4 percent for the Logan and 2 percent for *R. macropitalus*). Of 164 crosses of Logan × Mammoth only 2 were at all productive and these did not set fully; the remainder were entirely or nearly sterile. There were no contrasting characters on which to base a study of inheritance.

The Mammoth, like the Logan, was found to have 21 as its haploid chromosome number. Figure 4, A, shows a homotypic anaphase of Mammoth, and figure 4, B, shows a homotypic metaphase from a sport of Mammoth known as the Cory. Both figures show clearly the hexaploid chromosome number.

Eight F_1 hybrids between Logan and Mammoth were studied. Six of these have 21 as their haploid chromosome number. The chromo-

somes in some of these hexaploid plants were frequently unpaired in the early meiotic phases, and irregularities in chromosome distribution of later phases indicated the presence of incompatible chromosome sets. Figure 4, C, is a heterotypic prophase from one of these plants showing 20 bivalent and 2 unpaired chromosomes. Figure 4, D, shows a homotypic anaphase from a sister plant. This phase was found to be the most satisfactory for obtaining accurate chromosome counts if the chromosomes of the four groups were well sepa-

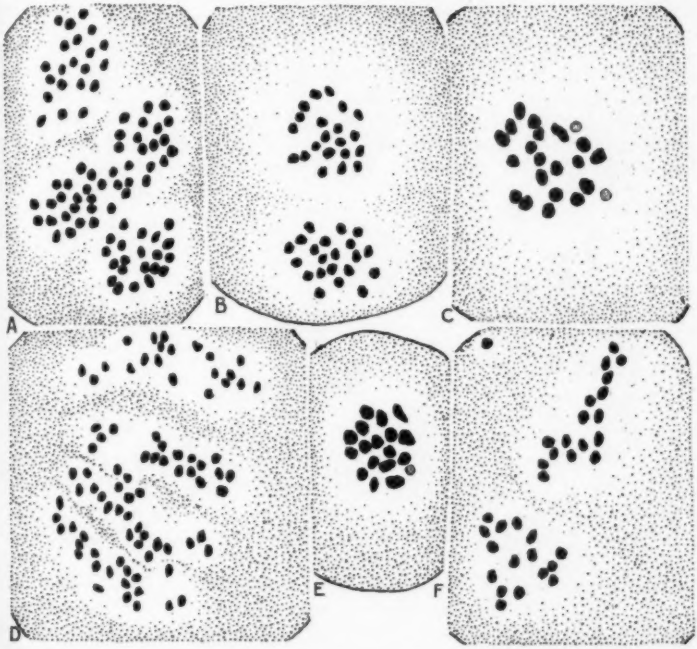


FIGURE 4.—Chromosomes in the Mammoth and in Logan × Mammoth hybrids: A, Homotypic anaphase in the Mammoth; B, homotypic metaphase in the Cory; C, heterotypic prophase in F_1 Logan × Mammoth hybrid (no. 12); D, homotypic anaphase in a sister hybrid plant (no. 10); E and F, heterotypic and homotypic metaphase, respectively, in pentaploid F_1 Logan × Mammoth hybrids (no. 7 and no. 4).

rated. At this stage there is no longer the difficulty of distinguishing between univalent and bivalent chromosomes.

Two plants from this group of hybrids were found to be pentaploid. These plants showed many irregularities in their chromosome distribution during the meiotic phases. Figure 4, E, is a typical heterotypic metaphase from plant 7, showing both univalent and bivalent chromosomes on the spindle. Figure 4, F, is a homotypic metaphase from plant 4, showing two major chromosome groups and an extended chromosome near the periphery of the cell.

The character of the pollen of these eight F_1 hybrids is shown in table 2. The percentage of sterility ranges from that of almost completely sterile plants to that of largely fertile plants. The two pentaploid plants were sterile, but the amount of aborted pollen in some of the hexaploid plants was large also, indicating that the incom-

patibility of the chromosomes from the two parents is sufficient in some plants to lead to the abortion of an appreciable amount of pollen, although the chromosome number is an even multiple of the basic number 7.

Logan × Young Hybrids

The Young, which originated as a cross of the Austin Mayes × Phenomenal (very similar to the Logan) in Louisiana, is a plant about as vigorous as the Logan. Its canes are slenderer and are even longer. Its fruit is large but intermediate in color between that of the Logan and that of the Austin Mayes.

Of 169 crosses of Logan × Young, 21 set half or more of their drupelets; the remainder were entirely or nearly sterile. No contrasting characters were apparent. Table 2 shows that in the nine hexaploid Logan × Young hybrids the amount of aborted pollen varied. In a few plants the amount was large, indicating that some of the chromosomes from the two parents were incompatible. The

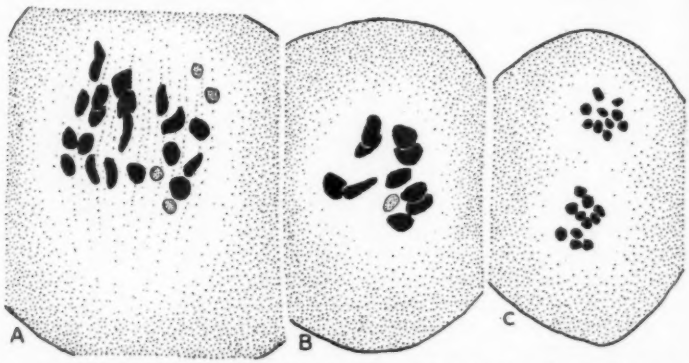


FIGURE 5.—Chromosomes in F_1 Logan × Young hybrids: A, Heterotypic prophase in plant no. 1; B, heterotypic prophase in triploid plant no. 7; C, homotypic metaphase in plant no. 7.

triploid plant was almost completely sterile, a condition usually found in triploid *Rubus*.

The Young likewise has 21 as its haploid number. Ten F_1 hybrids of the Logan × Young cross were studied cytologically. Of these, nine had 21 as their haploid chromosome number. The behavior of the chromosomes of these nine hexaploid hybrids during the reduction phases was less regular than that of hexaploid Logan seedlings, but more regular than that of some of the Logan × Mammoth hybrids.

Figure 5, A, shows a heterotypic prophase from plant no. 1. Four chromosomes are unpaired in this figure. At this phase unpaired chromosomes were frequently seen, but in many preparations the chromosomes were all paired and their distribution regular.

In plant 7 the chromosomes were exceptional in number and behavior. This plant had only 21/2 as its haploid chromosome number. The number of bivalents at diakinesis was variable, although most frequently there were 10 and a single univalent. Figure 5, B, shows a characteristic heterotypic prophase from the triploid plant.

At figure 5, C, is a homotypic metaphase showing 10 chromosomes on 1 plate and 11 on the other.

Logan × Lucretia Hybrids

The Lucretia, a horticultural variety of the eastern dewberry, likewise has 21 as its haploid chromosome number. Figure 6, A, shows 21 chromosomes on each plate of the homotypic metaphase from this variety. Of 19 crosses of the Logan × Lucretia 18 were sterile or nearly so, while 1 set a fair number of drupelets. Table 2 shows that the pollen condition of these crosses ranged from very little sterility to about 50 percent abortive pollen in the more sterile plants. The chromosome behavior and the large amount of sterile pollen in

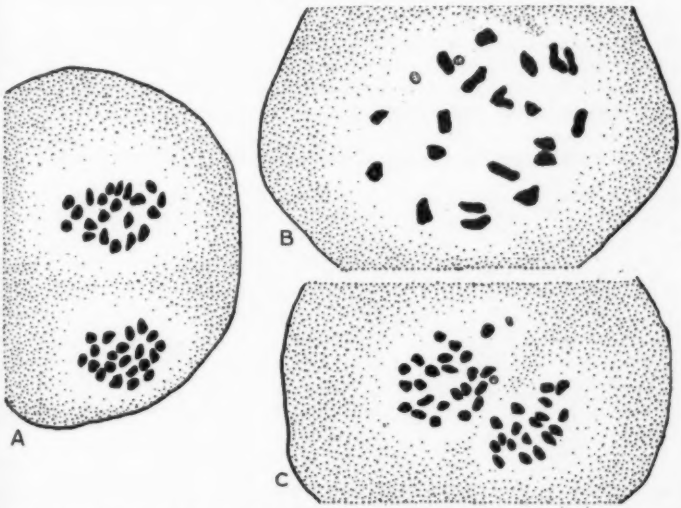


FIGURE 6.—Chromosomes in the Lucretia and in Logan × Lucretia hybrids: A, Homotypic metaphase in the Lucretia; B, diakinesis in Logan × Lucretia plant (no. 6); C, homotypic metaphase in Logan × Lucretia plant (no. 12).

some plants indicate that the chromosome complement of these plants is incompatible.

Nine F_1 Logan × Lucretia hybrids were studied and all were found to be hexaploid. The chromosomes of these few representative plants were variable in their behavior during meioses. In some plants many irregularities in chromosome pairing were observed, whereas in others it was unusual to find univalent chromosomes in the early heterotypic phases. Figure 6, B, shows a late diakinesis from plant 6, one of the more fertile plants. Figure 6, C, shows a homotypic metaphase from plant 12, one of the more sterile plants.

Rubus macropetalus × Logan Hybrids

Several plants that were said to have resulted from a cross of selections from the wild *Rubus macropetalus* and the Logan were observed in the garden of J. W. Ware in western Washington. The plants had

large canes and handsome wine-colored fruit. The color of the fruit was the same on all the plants, although the size ranged from about that of the Logan to somewhat smaller. The flavor of one sort was better than that of any wild berries tested.

Several seedlings, supposedly of this cross, also were seen at Cheshire, Oreg. One was male, several were pistillate, and several were perfect-flowered and had fruit of the same color as the Ware plants.

Still another berry, supposedly a cross of *Rubus macropetalus* × Logan, appeared as a seedling in a garden near Florence, Oreg. It likewise had wine-colored fruit nearly as large as the Logan and of very fine flavor. This cross, as well as those of Ware, was perfect-flowered.

Himalaya × Logan Hybrids

A few seedlings, all very much alike and said to be a cross of the Himalaya and the Logan, were seen at Ware's ranch. The plants were young but bore a few well-developed berries nearly black in color, of high flavor, and nearly as large as those of the Logan.

CHROMOSOMES IN OTHER WESTERN RUBUS FORMS

With a view to a better understanding of breeding problems and of the origin and evolution of the western species of *Rubus*, the chromosome numbers of other western species were obtained. The Himalaya, as previously determined (*1*), was found to have 14 as the haploid chromosome number; *Rubus spectabilis* Pursh, the salmonberry, 7; *R. parviflorus* Nutt., the thimbleberry, 7; and *R. leucodermis* Dougl., the western black raspberry, 7. The Lloyd George red raspberry has 7; the Cuthbert, 7, the Burbank Thornless (*R. inermis*, Willd., of Europe), 7; the Evergreen, 14; the Brainerd (Himalaya × an eastern blackberry), 21/2; and the Austin Thornless dewberry, 28.

DISCUSSION

In this western group of related forms of *Rubus* the haploid chromosome number ranges from 21 to 42. The members of the western group are distinct from other known groups of raspberries and blackberries in being dioecious. Dioeciousness has been found in only one other *Rubus* species, namely, *R. chamaemorus* L. (*9*), which has 28 chromosomes. It is interesting that dioecious species of *Rubus*, like dioecious species of *Fragaria*, occur only in forms with high chromosome numbers.

The haploid chromosome number (21) that characterizes the Logan is quite frequently found in *Rubus* species of the dewberry type. The behavior of the chromosomes of the Logan when associated with other *Rubus* varieties indicates that there is an appreciable amount of incompatibility between its chromosomes and those of the other varieties studied. In extreme cases this incompatibility leads to the production of very little viable pollen. No fully fertile crosses were obtained with the Young, the Lucretia, or even with the Mammoth, which like the Logan originated from a seedling of the Aughinbaugh and had 21 chromosomes. On the other hand, the supposed *Rubus macropetalus* × Logan crosses were fruitful.

Chromosome number is often indicative of the closeness of relationship of two species, but it seemed that a study of the behavior of the two chromosome sets when brought together in a hybrid plant might give a more satisfactory idea of the relationship of the two parent forms.

The chromosomes of the Logan show irregularities during meioses too infrequently to support the view that they are made up of two sets derived from *Rubus ursinus* and a red raspberry. In fact their behavior is no more irregular than that frequently found in a pure species.

If the Logan were of hybrid ancestry, with *Rubus macropetalus* as one parent, obviously its diploid number should exceed the haploid number of *R. macropetalus*. The haploid chromosome number of *R. macropetalus* is known only from the few collections made for this study. Neither 42, found in dioecious forms, nor 28, found in the Ideal Wild variety, are numbers that explain readily the presence of 42 somatic chromosomes in the Logan. It seems unnecessary to assume from either its chromosome number or its chromosome behavior that the Logan originated as a hybrid. From these considerations it seems probable that the Logan originated as a red-fruited perfect-flowered sport of the species herein designated as *R. loganobaccus*.

The discovery in the group of Logan × Young hybrids of one plant having the same chromosome number as the female parent suggests the possibility that *Rubus loganobaccus* is a haploid species derived from *R. ursinus* and *R. macropetalus*. However, it may be a survivor of former types that were pushed southward in glacial times.

Forms such as those collected in the wild and the Ideal Wild variety, having chromosome numbers intermediate between *R. loganobaccus* and *R. macropetalus*, may represent (1) remnants of *Rubus* species almost extinct, (2) hybrids between the three species discussed in this paper, or (3) aberrant forms of these species.

The excellent quality and fertility of the *Rubus macropetalus* × Logan crosses indicate the possibility of using for breeding purposes selected forms of all three species of western trailing blackberries.

SUMMARY

A characterization is given of the wild trailing blackberries, or dewberries, of the Pacific coast (*Rubus loganobaccus*, *R. ursinus*, and *R. macropetalus*), and a study of their chromosomes is made with reference to the origin and relationships of the cultivated varieties, particularly the Logan. A new variety of *R. ursinus* (var. *monophyllus*) is described.

Rubus macropetalus has 42 chromosomes as its haploid number; *R. loganobaccus*, 21. Plants taxonomically similar to *R. loganobaccus* were found to have 28 or 35 chromosomes. The cultivated variety Ideal Wild, thought to have originated as a cross between *R. macropetalus* and the Logan, has 28 chromosomes.

The history and cytology of the Logan variety are discussed. The chromosome number of the Logan is 21; of 11 seedlings, 1 had 35/2 and the other 10 had 21 chromosomes.

Breeding experiments with the Logan gave the following results: The F_1 seedlings of the selfed Logan showed characteristics of the

Logan and not of raspberry. Of the seedlings selected, some matured earlier and some later than the Logan; the fruit of some of these selections was sweeter than that of the Logan.

Crosses of the Logan (21 chromosomes) × Mammoth (21) gave 162 plants that were nearly or entirely sterile and 2 that were partially fertile. Of 8 plants examined, 6 had 21 chromosomes and 2 had 35/2 chromosomes.

Crosses of Logan × Young (21 chromosomes) gave 148 plants that were nearly or entirely sterile and 21 that were partially fertile. Of 10 plants examined 9 had 21 chromosomes and 1 had 21/2 chromosomes.

Crosses of Logan × Lucretia (21 chromosomes) gave 18 plants that were nearly or entirely sterile and 1 that was partially fertile. Each of 9 plants examined had 21 chromosomes.

Plants believed to be crosses between *Rubus macropetalus* (42 chromosomes) and the Logan (21) gave some perfect-flowered fertile seedlings.

Other western species (*Rubus spectabilis*, *R. parviflorus*, and *R. leucodermis*) have 7 chromosomes each.

From the data presented herein it is concluded that the Logan probably originated as a red-fruited perfect-flowered sport of *Rubus loganobaccus*.

LITERATURE CITED

(1) Anonymous
1916. Is the hybrid origin of the loganberry a myth? Jour. Heredity 7 : 504–507, illus.

(2) Bailey, L. H.
1923. Quidam rubi cultorum. Gentes Herbarum 1 : 139–200, illus.

(3) ———
1925. Rubus: enumeratio nativorum eubatorum in America septentrionali. Gentes Herbarum 1 : 203–300, illus.

(4) ———
1932. Eubati boreali-americani (Rubus subgen. Eubatus). Gentes Herbarum 2 : [270]–423, illus.

(5) Crane, M. B., and Darlington, C. D.
1927. The origin of new forms in Rubus I. Genetica 9 : [241]–[278], illus.

(6) ——— and Lawrence, W. J. C.
1929. Genetical and cytological aspects of incompatibility and sterility in cultivated fruits. Jour. Pomol. and Hort. Sci. 7 : 276–301, illus.

(7) Darrow, G. M.
1918. Culture of the Logan blackberry and related varieties. U.S. Dept. Agr. Farmers' Bul. 998, 24 p., illus.

(8) Kinney, L. F.
1897. The loganberry. R.I. Agr. Expt. Sta. Bul. 45, p. [67]-82, illus.

(9) Longley, A. E.
1926. Relationship of polyploidy to pollen sterility in the genera Rubus and Fragaria. Internatl. Conf. on Flower and Fruit Sterility. Mem. Hort. Soc. N.Y. 3 : 15–17.

(10) Rydberg, A.
1913. Rosaceae (pars). North Amer. Flora 22 (5) : 389–480.

EFFECT OF THE CALCIUM-PHOSPHORUS RELATIONSHIP OF THE RATION ON GROWTH AND BONE FORMATION IN THE PIG[1]

By R. M. Bethke, *associate (nutrition)*, B. H. Edgington, *associate in animal pathology*, and C. H. Kick, *assistant in nutrition, Department of Animal Industry, Ohio Agricultural Experiment Station*

INTRODUCTION

Many studies have been made on the need of calcium, phosphorus, and vitamin D in the nutrition of the pig. The majority of these investigations dealt with the effect of mineral and vitamin deficient rations and how the deficiencies could be corrected. No specific information, so far as the writers are aware, is available regarding the effect of the calcium-phosphorus ratio of the ration on its relation to vitamin D on growth and bone formation in the pig. A study was therefore made of this phase of the subject, and the results are reported in the present paper.

REVIEW OF LITERATURE

McCollum and his associates (*6, 9*)[2] and Sherman and Pappenheimer (*8*) pointed out independently that the quantitative relation between the calcium and phosphorus in the food supply was, within certain limits of concentration, of great importance in determining whether an animal, like the rat, developed normal or pathological bones. Bethke, Steenbock, and Nelson (*3*) reported that the amount of antirachitic factor required by rats on a synthetic ration containing 0.655 percent of phosphorus varied inversely with the calcium content of the ration. This indicates the existence of a quantitative relation between vitamin D and calcium in effecting the utilization of the latter. More recent investigations at this station (*2*) revealed that the amount of vitamin D required by the rat is directly correlated with the calcium and phosphorus content of the ration and the ratio in which these elements are present. Evidence was also obtained which showed that increased levels or concentrations of calcium and phosphorus in the ration exerted beneficial effects on growth and on bone ash, but the effects were not so great as those exerted by the ratio of calcium to phosphorus. Similar observations (*1*) have been made with the chick. Haag and Palmer (*5*) also showed the importance of a more or less balanced condition of calcium, phosphorus, and magnesium salts in the ration for good growth and mineral retention in the rat. The same investigators also called attention to the importance of the vitamin-mineral interrelationship in the nutrition of the rat.

The importance of ample quantities of calcium and phosphorus in the ration of the pig has been shown many times. Maynard, Goldberg, and Miller (*7*) reported that even when calcium and phosphorus were in abundance in the ration of the pig, poor bone development

[1] Received for publication Feb. 13, 1933; issued September 1933.
[2] Reference is made by number (italic) to Literature Cited, p. 338.

frequently resulted which could be corrected by supplying vitamin D or its equivalent. Bohstedt et al. (*4*), at this station, also observed that under certain conditions improperly calcified bones occurred, even though the ration in question was supplemented with what was supposed to be ample quantities of calcium. Observations of practical farm feeding have indicated that large amounts of calcium in the form of calcium carbonate or ground limestone in the grain rations of pigs often produce unfavorable results.

EXPERIMENTAL PROCEDURE

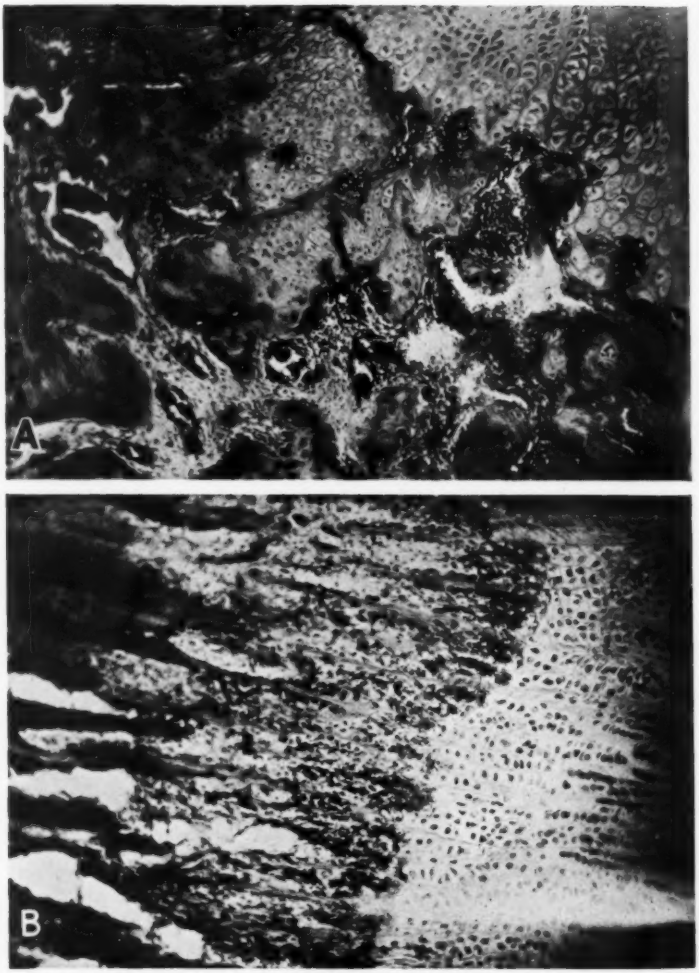
The findings and observations of these workers led the writers to investigate the importance of the calcium-phosphorus ratio in the nutrition of the rat and the pig. For experimental reasons, it was deemed advisable to use identical rations with the two species. A ration was desired that could be relied upon to produce incipient rickets in the rat in 3 to 5 weeks and that would also constitute a comparatively practical ration for the pig. After considerable preliminary investigation, a basal ration of 79.5 parts yellow corn, 20.0 parts soybean meal, and 0.5 part sodium chloride was adopted. This ration, when properly supplemented with minerals, had given good results in other studies with pigs. The same basal ration was used in the different experiments. The present report includes only the results of three experiments with pigs.

Five lots of six pigs each were used in the first experiment. The pigs were started on experiment shortly after weaning and were from 20 to 35 pounds in weight. All lots were housed in a central building provided with concrete floors. One lot had access to an outdoor paved runway, on which they were fed. A second lot had access to an outdoor dirt paddock but, like the other three lots, were fed indoors. The pigs were self-fed their respective rations for a period of 19 weeks, starting the latter part of June. At the end of the experiment all animals were slaughtered and given a routine postmortem examination. Portions of ribs, including the costochondral junctions and both femurs, were removed from each pig for histological study and ash analysis. The average growth of the different lots is shown in figure 1. Table 1 shows the average daily feed consumption and the average breaking strength and ash analysis of the femurs. The percentage of ash is expressed on a moisture-free and fat-free basis.

TABLE 1.—*Effect of the calcium-phosphorus ratio of the ration on calcification in the pig*

Lot no.	Additions to basal ration	Calcium and phosphorus in ration	Calcium-phosphorus ratio in ration	Average daily feed	Average weight of femurs	Average breaking strength	Average ash in femurs
		Percent		*Pounds*	*Grams*	*Pound*	*Percent*
[a] 1	None	Ca, 0.06; P, 0.33	0.18	1.52	58.7	171±13	49.5±0.72
2	3 parts calcium carbonate	Ca, 1.16; P, 0.32	3.62	1.88	58.0	143±23	46.0± .63
3	3 parts calcium carbonate, 3 parts disodium phosphate.	Ca, 1.14; P, 0.62	1.84	3.08	111.7	709±51	61.4± .39
4	1 part ground limestone, 1 part bone meal (outdoor dirt runway).	Ca, 0.62; P, 0.44	1.41	3.09	124.9	791±30	61.1± .33
5	3 parts calcium carbonate (outdoor paved runway).	Ca, 1.16; P, 0.32	3.62	2.77	80.5	321±38	52.5± .41

[a] 1 pig dead in lot; averages based on 5 animals.



PHOTOMICROGRAPHS OF THE COSTOCHONDRAL JUNCTION OF PIGS.

A, No. 24, lot 2, experiment 1, showing distorted calcification resembling rickets. B, No. 8, lot 3, experiment 1, showing normal calcification.

The pigs on the basal ration (lot 1) exhibited marked evidence of a mineral deficiency, in the form of a stiffened, staggering gait. Several individuals in this lot were so severely affected that they were unable to walk. One of these died 2 days prior to the termination of the experiment. Another pig in this lot died early in the experiment from a ruptured bladder. Two showed signs of tetany—undoubtedly due to a low calcium intake. The addition of 3 parts of calcium carbonate

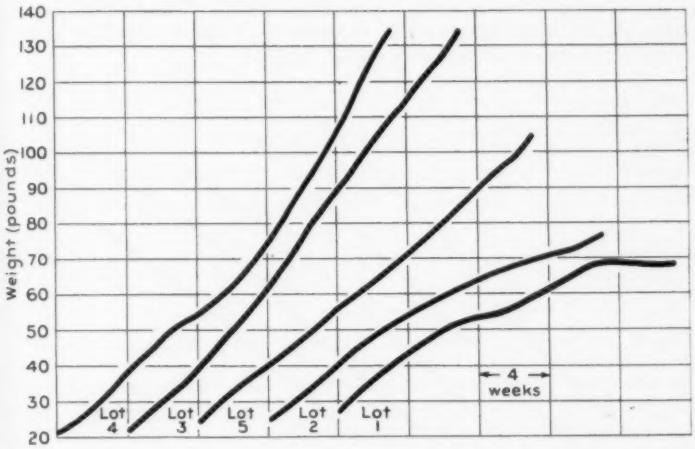


FIGURE 1.—Average growth of different lots of pigs in experiment 1: Lot 1, basal ration only; lot 2, basal ration plus 3 parts calcium carbonate; lot 3, basal ration plus 3 parts calcium carbonate and 3 parts disodium phosphate; lot 4, basal ration plus 1 part ground limestone and 1 part bone meal (outdoor dirt runway); lot 5, basal ration plus 3 parts calcium carbonate (outdoor paved runway).

to the basal ration (lot 2), while causing an approximate twentyfold increase in calcium intake, did not improve the ration for growth or bone formation. All the pigs in this lot showed marked clinical symptoms of rickets, the diagnosis being further supported by the ash determinations of the femurs and the histological examination of the costochondral junctions (pl. 1, A). Changing the calcium-phosphorus ratio of the ration from 3.62 (lot 2) to 1.84 (lot 3) by the addition of 3 parts disodium phosphate resulted in increased feed intake, improved growth, and a normal breaking strength and ash content of the femurs. The costochondral junctions of the pigs from lots 3 and 4 also showed normal calcification (pl. 1, B). The beneficial effects of direct sunlight on growth and calcification are revealed in the results in lot 5. However, it is apparent that the physiological rays were not sufficient entirely to counteract the faults of the wide calcium-phosphorus ratio (3.62) and produce bones having a normal ash value and histological structure.

The results of the first experiment indicated that the calcium-phosphorus ratio of the ration exerted an effect on feed consumption and on bone calcification in the pig. To confirm the data already presented, and to obtain additional knowledge with respect to the effect of the calcium-phosphorus ratio on bone formation, a second experiment was initiated. The basal ration was the same as that used

in the first experiment but was supplemented with calcium and phosphorus in such quantities that the pigs in each lot received a ration possessing a different proportion of calcium to phosphorus. The trial was conducted during the winter months and involved 9 lots of 6 pigs each. These pigs weighed from 20 to 35 pounds at the beginning of the test. All lots were confined indoors and self-fed their respective rations. Straw was used for bedding. The experiment was continued for 18 weeks, when the animals were slaughtered and examinations made as in the previous trial. The rations and the results of the bone studies are presented in table 2. The average growth of the different lots is shown in figure 2.

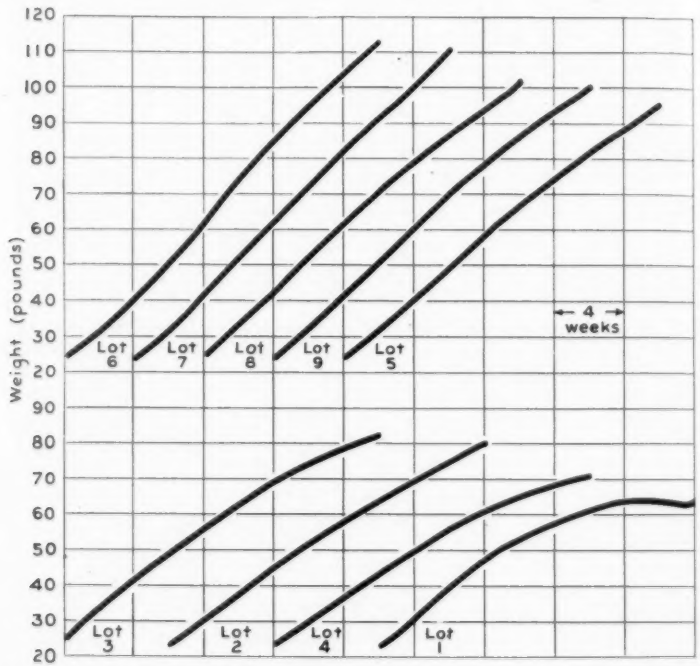


FIGURE 2.—Average growth of different lots of pigs in experiment 2: Lot 1, basal ration only; lot 2, basal ration plus 1 part calcium carbonate; lot 3, basal ration plus 2 parts calcium carbonate; lot 4, basal ration plus 3 parts calcium carbonate; lot 5, basal ration plus 3 parts calcium carbonate and 1 part disodium phosphate; lot 6, basal ration plus 3 parts calcium carbonate and 2 parts disodium phosphate; lot 7, basal ration plus 3 parts calcium carbonate and 3 parts disodium phosphate; lot 8, basal ration plus 2 parts calcium carbonate and 3 parts disodium phosphate; lot 9, basal ration plus 2 parts tricalcium phosphate.

The pigs on the basal ration, or the basal ration supplemented with varying amounts of calcium carbonate (lots 1, 2, 3, and 4) showed extreme symptoms of mineral deficiency. All the pigs in these lots, with the exception of three individuals in lot 3, were so severely affected that they were unable to walk. This necessitated placing their feed and water before them in small troughs. The pigs in the other lots (lots 5, 6, 7, 8, and 9), which received the basal

ration supplemented with different amounts of calcium and phosphorus, did not exhibit such extreme symptoms of a deficiency, although the individual pigs in these lots all showed varying degrees of stiffness in the latter part of the experiment.

TABLE 2.—*The effect of the calcium and phosphorus content of the ration on bone formation of pigs*

Lot no.	Additions to basal ration	Calcium and phosphorus in ration	Calcium-phosphorus ratio in ration	Average daily feed	Average weight of femurs	Average breaking strength	Average ash in femurs
		Percent		*Pound*	*Gram*	*Pound*	*Percent*
1	None	Ca, 0.06; P, 0.33	0.18	1.35	42.2	124±21	44.9±0.71
2	1 part $CaCO_3$	Ca, 0.42; P, 0.33	1.27	1.90	52.2	143±12	46.3± .46
3	2 parts $CaCO_3$	Ca, 0.79; P, 0.32	2.47	1.95	54.5	173±15	48.2± .57
4	3 parts $CaCO_3$	Ca, 1.16; P, 0.32	3.62	1.55	48.2	149±18	46.9± .60
5	3 parts $CaCO_3$; 1 part Na_2HPO_4 .12 H_2O.	Ca, 1.16; P, 0.43	2.70	2.40	67.5	287±26	54.0± .91
6	3 parts $CaCO_3$; 2 parts Na_2HPO_4 .12 H_2O.	Ca, 1.15; P, 0.54	2.13	2.70	82.0	573±59	58.2± .57
7	3 parts $CaCO_3$; 3 parts Na_2HPO_4 .12 H_2O.	Ca, 1.14; P, 0.64	1.78	2.72	91.5	493±53	55.6± .73
8	2 parts $CaCO_3$; 3 parts Na_2HPO_4 .12 H_2O.	Ca, 0.78; P, 0.64	1.22	2.52	72.1	423±42	55.1± .45
9	2 parts $Ca_3(PO_4)_2$	Ca, 0.83; P, 0.73	1.14	2.41	71.5	384±37	55.9± .50

The results of the bone studies (table 2) show that the ratio of calcium to phosphorus and the amounts of these elements in the ration had a marked effect on the breaking strength and the percentage of ash in the femurs. The addition of 2 parts of calcium carbonate, or a change in the calcium-phosphorus ratio from 0.18 to 2.47 caused a significant increase in the percentage of ash, whereas further additions of calcium carbonate, with a widening of the calcium-phosphorus ratio to 3.62, decreased the ash content and breaking strength. Although the decreases in ash content and breaking strength are not statistically significant, they indicate that the ration became more rachitic upon the further addition of calcium and the widening of the calcium-phosphorus ratio. The inclusion of both phosphorus and calcium in the ration caused a significant increase in ash content and in the breaking strength of the femurs. It is apparent that phosphorus, as well as calcium, and the proportion in which they are present in the ration may serve as limiting factors in calcification processes. The data also suggest that the requirements of the pig for vitamin D can be minimized by properly adjusting the calcium and phosphorus content of the ration. Although no vitamin D fed lots were included in the trial, it is obvious that a ration which causes bones to have an ash content between 55 to 60 percent will not require so much of the antirachitic factor for normal calcification as will one that causes bones to have 45 to 55 percent of ash. The results of the histological examinations of the costochondral junctions confirmed the bone-ash data.

It is of interest to note that, in general, the ash values of the second experiment are lower than those of the first. The writers are of the opinion that this difference is primarily due to vitamin D storage and control. The pigs used in the last test were farrowed in October and started on test in December; whereas those in the first experiment were farrowed in April and had access to May and June sunshine before they were started on experiment the latter part of June.

The results of the two previous experiments conclusively showed that bone formation in the pig was influenced by the calcium-phosphorus ratio of the ration. It still remained to be determined whether the level or concentration of calcium and phosphorus at different ratios would exert an effect on bone formation. Accordingly, a third experiment, comprising 10 lots of 6 pigs each, was started. The pigs used were farrowed in January and had access to the outdoors prior to the start of the experiment in April. They were treated for worms and immunized against cholera before being placed on test. All lots were confined indoors in concrete paved pens and self-fed their respective rations. The experiment ran for 112 days, when the animals were killed for post-mortem examination. Femurs and costochondral junctions were saved for examination, as in the previous experiments. Two days prior to the termination of the experiment, the blood of the individual pigs was analyzed for calcium by the Clark and Collip procedure and for inorganic phosphorus by the method of Briggs. The blood was obtained by tail bleeding and allowed to refrigerate overnight before the serum was drawn off for analysis.

The yellow corn-soybean meal ration was supplemented with such amounts of calcium carbonate and steamed bone meal as to obtain approximately the same three calcium-phosphorus ratios at three different concentrations. In order to have a vitamin D fed lot for comparison, the same ration as fed to lot 5 was supplemented with 0.5 part of aerated cod-liver oil and fed to lot 10. The aerated cod-liver oil was potent in vitamin D but practically devoid of vitamin A.

TABLE 3.—*Effect of a varying calcium and phosphorus intake on growth, feed utilization, blood composition, and bone formation in the pig*

Lot no.	Additions to ration		Calcium in ration	Phosphorus in ration	Calcium-phosphorus ratio	Average initial weight of animals	Average gain in weight	Average daily gain
	$CaCO_3$	Steamed bonemeal						
	Parts	*Parts*	*Percent*	*Percent*		*Pounds*	*Pounds*	*Pounds*
1	0.7		0.33	0.33	1.0	37.2	109.5	0.98±0.050
2	1.6		.64	.32	2.0	37.5	112.8	1.01± .034
3	2.6		1.05	.31	3.4	38.8	77.1	.69± .062
4[a]	.2	1	.47	.46	1.0	35.2	126.0	1.16± .025
5	1.5	1	.92	.45	2.0	34.7	131.8	1.18± .030
6	2.8	1	1.36	.45	3.0	37.3	116.3	1.04± .038
7		2	.72	.60	1.2	37.8	142.8	1.27± .033
8	1.3	2	1.16	.58	2.0	39.0	142.1	1.27± .029
9	3.1	2	1.75	.57	3.0	33.0	144.5	1.29± .038
10[b]	1.5	1	.92	.45	2.0	36.2	159.0	1.42± .045

Lot no.	Average daily feed	Feed intake per 100 pounds of gain	Blood analysis[c]		Average weight of femurs	Average breaking strength	Average ash in femurs	Degree of calcification[d]
			Ca in serum	P in serum				
	Pounds	*Pounds*	*Milligrams*	*Milligrams*	*Grams*	*Pounds*	*Percent*	
1	3.22	329.1	10.6	4.4	106	439±38	57.7±0.70	14
2	3.61	358.8	11.4	4.4	104	433±18	57.3± .66	15
3	2.50	364.8	11.1	4.9	96	351±37	55.4± .63	10
4	3.82	330.3	11.0	6.6	137	632±33	60.6± .59	20
5	3.94	334.9	11.6	6.5	133	801±51	63.5± .27	23
6	3.72	358.0	11.3	5.8	128	708±26	60.1± .48	22
7	4.38	343.5	10.3	6.3	151	785±5	62.8± .43	21
8	4.47	352.4	10.4	6.4	152	861±40	62.1± .52	24
9	4.30	333.6	11.5	6.6	142	898±29	62.3± .07	22
10[b]	4.38	309.0	11.4	6.4	163	812±16	62.4± .28	24

[a] 1 pig died after being on experiment 13 weeks, from fracture of both illia.
[b] 0.5 part of aerated cod-liver oil included in ration.
[c] Expressed in mg per 100 cc of serum.
[d] A score of 24 indicates normal calcification, and in descending order abnormality.

The growth and feed records are presented in table 3. It is evident that by using a ration having a calcium-phosphorus ratio of 3.0, with a phosphorus content of 0.31 or 0.45 percent, the rate of gain is significantly decreased and the feed utilization per unit of gain slightly increased over the lower ratios. This, however, was not observed when the phosphorus was increased to approximately 0.60 percent. It appears from these observations that phosphorus as well as the calcium-phosphorus ratio was a limiting factor at the two lower concentrations. This is particularly apparent when the performance of lots 1, 2, and 3, which were fed a ration with a phosphorus content of about 0.31 percent, are compared with lots 4, 5, and 6, which had about 0.45 percent of phosphorus in their ration. The beneficial effects of aerated cod-liver oil on growth and feed utilization are revealed by comparing the results of lots 5 and 10. The writers are not certain that the increased gains and better feed utilization are entirely due to vitamin D. Other unpublished data suggest that some other factor in the cod-liver oil, aside from vitamin D, might have exerted a favorable influence.

The results of the blood and bone analysis, also presented in table 3, show that the inorganic phosphorus content of the blood serum, and the breaking strength and ash content of the femurs from the animals in lots 1, 2, and 3 were below normal. It is thought that these results indicate that phosphorus was a limiting factor, since an increase in the phosphorus content of the ration, irrespective of the amount of calcium present, resulted in a significant improvement. The blood and bone data, in this respect, corroborated the growth and feed-utilization results shown in table 3.

The effects of the calcium-phosphorus ratio on bone formation are not so apparent in this trial as in the previous experiments. However, the data in general support the previous observations that the calcium-phosphorus ratio, within certain limits of concentration, influences calcification. The experiment also shows that the concentration of calcium and phosphorus in the ration is a factor in growth and bone formation. When the percentage of these elements in the ration was increased, normal blood and bone composition resulted, irrespective of the ratio or the presence of added vitamin D. The data, in general, show that it is possible to so regulate the amount and proportion of calcium to phosphorus in the ration of the pig as to minimize the requirements for the antirachitic vitamin for normal growth and bone formation.

The results of the histological examinations (table 3) of the costochondral junctions substantiated the results of the ash analysis. For the sake of comparison, the results are expressed numerically. These figures were arrived at by arbitrarily assigning a certain score to the degree of calcification in each pig and then totaling the same for each lot. On this basis a score of 24 would indicate normal calcification throughout the lot, and in descending order an abnormal calcification, suggestive of rickets.

8822—33——6

SUMMARY

The calcium-phosphorus ratio of the ration is a factor in growth and bone formation in the pig. In general, best results were obtained with a calcium-phosphorus ratio between 1.0 and 2.0. When the proportion of calcium to phosphorus was greater than 3.0, the pigs became more rachitic and the requirements for vitamin D were increased.

The concentration of calcium and phosphorus in the ration also exerted an effect on growth and bone formation.

Phosphorus, as well as calcium, may be a limiting factor in growth and calcification. Evidence was obtained indicating that the phosphorus content of the ration should not be less than approximately 0.60 percent for good growth and bone formation in the absence of added vitamin D.

The requirement of the pig for vitamin D can be minimized by properly adjusting the calcium and phosphorus content of the ration.

LITERATURE CITED

(1) Bethke, R. M., Kennard, D. C., Kick, C. H., and Zinzalian, G.
1929. The calcium-phosphorus relationship in the nutrition of the growing chick. Poultry Sci. 8 : 257–265.

(2) ——— Kick, C. H., and Wilder, W.
1932. The effect of the calcium-phosphorus relationship on growth, calcification, and blood composition of the rat. Jour. Biol. Chem. 98 : 389–403.

(3) ——— Steenbock, H., and Nelson, M. T.
1923. Fat-soluble vitamins. XV. Calcium and phosphorus relations to growth and composition of boood and bone with varying vitamin intake. Jour. Biol. Chem. 58 : 71–103, illus.

(4) Bohstedt, G., Bethke, R. M., Edgington, B. H., and Robison, W. L.
1926. Mineral and vitamin requirements of pigs. (Experiments IV to VIII). Ohio Agr. Expt. Sta. Bul. 395 : 99–229, illus.

(5) Haag, J. R., and Palmer, L. S.
1928. The effect of variations in the proportions of calcium, magnesium, and phosphorus contained in the diet. Jour. Biol. Chem. 76 : 367–389, illus.

(6) McCollum, E. V., Simmonds, N., Parsons, H. T., Shipley, P. G., and Park, E. A.
1921. Studies on experimental rickets. I. The production of rachitis and similar diseases in the rat by deficient diets. Jour. Biol. Chem. 45 : 333–341, illus.

(7) Maynard, L. A., Goldberg, S. A., and Miller, R. C.
1925. A study of the dietary relationships and the pathology of "stiffness" in swine. N. Y. (Cornell) Agr. Expt. Sta. Mem. 86, 34 p., illus.

(8) Sherman, H. C., and Pappenheimer, A. M.
1921. A dietetic production of rickets in rats and its prevention by an inorganic salt. Soc. Expt. Biol. and Med. Proc. 18 : 193–197.

(9) Shipley, P. G., Park, E. A., McCollum, E. V., Simmonds, N., and Parsons, H. T.
1921. Studies on experimental rickets. II. The effect of cod liver oil administered to rats with experimental rickets. Jour. Biol. Chem. 45 : 343–348, illus.

PHYSIOLOGIC SPECIALIZATION OF SPHACELOTHECA CRUENTA (KÜHN) POTTER[1]

By L. E. MELCHERS[2]

Head, Department of Botany, Kansas Agricultural Experiment Station

INTRODUCTION

The loose kernel smut, *Sphacelotheca cruenta* (Kühn) Potter, is occasionally found in small quantities in fields of sorghum, *Sorghum vulgare* Pers., although it is not widely distributed over the United States. An account of its discovery, its geographic distribution, and the morphologic characters of the causal organism have been adequately discussed (*4*, *6*, *8*).[3] While *S. cruenta* is much less destructive in America than the fungus causing covered kernel smut of sorghum, *Sphacelotheca sorghi* (Link) Clinton, it is of scientific interest because it is known to hybridize with the latter (*7*, *8*).

No extensive test to determine the pathogenicity of *Sphacelotheca cruenta* to different varieties of sorghum has been reported, although general observations on varietal response have been made by Reed (*5*). In 1918 Kulkarni (*1*) obtained seed of milo from the United States and inoculated it with spores of *S. sorghi* and *S. cruenta* from India. He reported that out of a total of 645 heads obtained, 3 were attacked by *S. sorghi* (0.47 percent infection) and 50 by *S. cruenta* (7.8 percent infection). Unquestionably Kulkarni's results for both *S. sorghi* and *S. cruenta* were authentic[4] and in the light of present knowledge he undoubtedly was dealing with physiologic forms of the two species of sorghum kernel smut which differed from those common in the United States. At the time of his publication, however, specialization in the smut fungi had not been reported.

METHODS AND MATERIALS

In 1928 C. H. Ficke found a specimen of loose kernel smut in a field containing many varieties of sorghum. The discovery was of particular interest for two reasons: (1) But one head of loose kernel smut was found although there was an abundance of covered kernel smut in the field, and (2) the diseased head was that of a feterita plant, a sorghum resistant to practically all forms of *Sphacelotheca sorghi* and hitherto reported as highly resistant to attacks of *S. cruenta*. Martin and Ratliffe (*2*) recently reported some plants of feterita attacked by *S. cruenta*. In one other instance a feterita plant was reported to be attacked by the loose kernel smut (*8*), but no studies were made although the authors suspected that it might be explained on the basis of physiologic specialization.

In 1929, the smut collected by Ficke was increased so as to provide sufficient inoculum for varietal studies. In 1930 a specimen of

[1] Received for publication Apr. 3, 1933; issued September 1933. Contribution no. 331, department of botany, Kansas State College of Agriculture and Applied Science.

[2] The writer gratefully acknowledges the assistance given by C. O. Johnston, C. H. Ficke, F. B. Bosley, and C. A. Wismer in these investigations.

[3] Reference is made by number (italic) to Literature Cited, p. 342.

[4] This smut, according to Reed, was originally obtained in 1921 or 1922 from S. L. Ajreker, Poona Agricultural College, Poona, India. The specimen obtained from Reed in 1930 was on Black Amber sorgo.

Sphacelotheca cruenta was obtained through the courtesy of G. M. Reed, of the Brooklyn Botanic Garden, N.Y.[4] These two collections of the loose kernel smut were used in the varietal studies herein reported. The experiments were conducted in the field at Manhattan, Kans., during the years 1930–32, inclusive.

The smut reaction of 35 varieties of sorghum was studied. Not all of these varieties were grown in 1930 and 1931, however. Self-pollinated seed[5] was used to insure purity of the variety. The same methods of inoculating seed, planting, and keeping field records were used as had previously been employed in the varietal studies with *Sphacelotheca sorghi* (*3*, *6*). From 100 to 150 plants of each variety constituted a row. The relative susceptibility of the variety was determined from the number of smutted plants that appeared in the row.

EXPERIMENTAL RESULTS

The results of 3 years' work are presented in table 1. On the basis of resistance and susceptibility, the different varieties of sorghum have been arranged arbitrarily in four groups, A, B, C, and D. Environmental conditions in 1931 and 1932 were apparently not so favorable for infection as in 1930, for the percentages of infection were appreciably lower in practically all varieties.

It will be noted that two distinct physiologic forms of *Sphacelotheca cruenta* were found. The form obtained from India is designated form 1, and that discovered at Manhattan, form 2. Kafir × feterita K.B. 2686 and Pierce kaferita K.B. 2547 are resistant to form 2, whereas these varieties are readily attacked by form 1. On the other hand, form 2 attacks Red Amber × feterita K.B. 2570 and K.B. 2501, and White Yolo K.B. 2525 very readily, whereas form 1 infected but 1 plant out of nearly 1,000 inoculated.

In general, the milos, feteritas, hegari, and Dwarf Shantung kaoliang are extremely resistant to both forms; the studies thus far made indicate that they are immune.

The varieties in group B, which includes Dwarf Yellow milo, certain feteritas, feterita hybrids, Fargo Straightneck milo, Grohoma, and White durra, are only slightly susceptible to both forms of *Sphacelotheca cruenta*.

Group C, consisting of Premo, Red Amber, shallu, and Weskan, is highly susceptible to both forms of the organism.

Group D comprises a number of varieties which may be susceptible to one form and resistant to the other. Several varieties in this group, it will be noted, may be used as differential varieties in separating form 1 from form 2.

The results of these tests show conclusively that the loose kernel smut of sorghum obtained from India is distinct from that collected at Manhattan. At present it is not known whether there are additional physiologic forms of *Sphacelotheca cruenta*, but it seems very probable that other forms could be determined if new collections of the smut were available and the range of sorghum varieties extended.

In hybridization studies by Rodenhiser (*7*) in which he crossed *Sphacelotheca sorghi* with *S. cruenta*, the collections of *S. cruenta* which were supplied by the writer and referred to by Rodenhiser as C1 and C2, are here reported as physiologic forms 1 and 2.

[4] See footnote 4, p. 339.

[5] Members of the Department of Agronomy kindly furnished seed of some varieties.

TABLE 1.—*Summary of reaction of sorghum varieties to 2 physiologic forms of Sphacelotheca cruenta, Manhattan, Kans., 1930–32*

[Percentage of plants showing smut of form indicated]

Group and variety	K.B.[a] no.	Form 1				Form 2			
		1930	1931	1932	Average	1930	1931	1932	Average
Group A:									
Spur feterita	2540	0	0	0	0	0	0	0	0
Dwarf Yellow milo, row no. 3, 1924	2515	0	0	0	0	0	0	0	0
Standard Yellow milo	2524	----	----	0	0	----	----	0	0
Standard White milo	2533	----	----	0	0	----	----	0	0
Dwarf Yellow milo × Pink	2693	----	0	0	0	----	0	0	0
Hegari selection	2537	0	0	0	0	0	0	0	0
Do	2518	0	0	0	0	0	0	0	0
Schrock selection	2541	----	----	0	0	----	----	0	0
Dwarf Shantung kaoliang, C.I.[a] 293	2565	----	----	0	0	----	----	0	0
Group B:									
Dwarf Yellow milo, C.I. 332	2555	0	0	0	0	0	0	1.1	.4
Red Leaf feterita	2543	0	10	0	3.3	0	0	0	0
Feterita hybrid	2687	8.4	0	2.8	3.7	0	.7	0	.2
Feterita, S.P.I.[a] 51989	2690	7.1	4.4	0	3.8	1.4	2	0	1.1
Fargo Straightneck milo	2677	2.3	0	0	.8	0	0	4.1	1.4
Red Amber × feterita, row no. 56	2573	0	0	0	0	3.9	0	0	1.3
Red Amber × feterita, row no. 25	2562	0	0	0	0	15.6	0	0	5.2
Grohoma	3032	----	5.1	8.6	6.9	----	3.3	1.5	2.4
White durra	2528	----	----	1.2	1.2	----	----	3.5	3.5
Group C:									
Premo	2688	0	26.2	15.9	14.0	20.3	12.0	12.5	14.9
Red Amber	32313	----	----	15.6	15.6	----	----	16.0	16.0
Shallu	2542	90.2	31.0	33.6	51.6	52.6	18.5	29.5	33.5
Weskan	2522	----	----	45.3	45.3	----	----	46.2	46.2
Group D:									
Early White milo	3026	----	----	10.5	10.5	----	----	0	0
Pierce kaferita	2547	59.4	10.4	0	23.3	0	1.4	0	.5
Kafir × feterita	2686	47.6	9.0	11.2	22.6	0	1.1	0	.4
Kafir × milo 26-3-1-1	2561	63.2	10.0	0	24.4	1.7	0	0	.6
Manchu Brown kaoliang	2568	44.8	16.0	2.5	21.1	6.9	2.6	4.6	4.7
Darso	3003	44.2	19.3	5.0	22.8	6.8	3.9	8.8	6.5
White darso	3002	43.8	49.6	9.4	34.3	7.6	10.0	12.0	9.9
Acme broomcorn	2558	88.0	12.5	8.2	36.2	20.0	8.3	4.0	10.8
Kansas Orange	3048	85.1	36.0	9.5	43.5	19.5	6.9	17.7	14.7
Blackhull	3025	50.8	23.6	16.6	30.3	29.9	5.7	10.7	15.4
Red Amber × feterita, row no. 57	2570	0	0	0	0	30.3	1.2	3.6	11.7
Red Amber × feterita, row no. 12	2501	0	0	0	0	47.5	3.1	8.9	19.8
White Yolo	2525	1.9	0	0	.6	21.7	14.1	5.2	13.6

[a] K.B., C.I., and S.P.I. indicate, respectively, accession numbers of the department of botany, Kansas Agricultural Experiment Station, Division of Cereal Crops and Diseases, and Division of Foreign Plant Introduction, U.S. Department of Agriculture.

It is apparent that *Sphacelotheca sorghi* and *S. cruenta* are equally virulent on some varieties of sorghum. A larger number of the so-called resistant sorghums are attacked by *S. sorghi*, however, because of the presence of five physiologic forms of that organism (*3*).

SUMMARY

Two physiologic forms of *Sphacelotheca cruenta* have been found, and these are designated forms 1 and 2. They may be separated on the basis of their pathogenicity to various sorghums.

Certain of the feteritas, milo, hegari, Schrock, and Dwarf Shantung kaoliang are highly resistant to both forms.

Form 1 attacks kafir × feterita and Pierce kaferita very readily, while form 2 does not infect these varieties to any extent. On the other hand, form 2 attacks Red Amber × feterita and White Yolo heavily, while these sorghums are immune from form 1.

Thirty-five varieties of sorghums were tested over a 3-year period, but not all were grown in 1930 and 1931. These studies indicate that

certain varieties of feterita and milo generally regarded as immune may be attacked by one or both forms of *S. cruenta*.

It is believed that other forms of *S. cruenta* may be found if additional collections of this smut are tested on a more extensive group of sorghums.

LITERATURE CITED

(1) KULKARNI, G. S.
1918. SMUTS OF JOWAR (SORGHUM) IN THE BOMBAY PRESIDENCY. Agr. Research Inst., Pusa, Bul. 78, 26 p., illus.

(2) MARTIN, J. H., and RATLIFFE, G. T.,
1927. LOOSE KERNEL SMUT ON FETERITA. (Phytopathological note) Phytopathology 17: 338–339.

(3) MELCHERS, L. E., FICKE, C. H., and JOHNSTON, C. O.
1932. A STUDY OF THE PHYSIOLOGIC FORMS OF KERNEL SMUT (SPHACELOTHECA SORGHI) OF SORGHUM. Jour. Agr. Research 44: 1–11, illus.

(4) POTTER, A. A.
1915. THE LOOSE KERNEL SMUT OF SORGHUM. Phytopathology 5: [149]–154, illus.

(5) REED, G. M.
1923. VARIETAL RESISTANCE AND SUSCEPTIBILITY OF SORGHUMS TO SPHACELOTHECA SORGHI (LINK) CLINTON AND SPAHCELOTHECA CRUENTA (KÜHN) POTTER. Mycologia 15: 132–143, illus.

(6) ——— and MELCHERS, L. E.
1925. SORGHUM SMUTS AND VARIETAL RESISTANCE IN SORGHUMS. U.S. Dept. Agr. Bul. 1284, 56 p., illus.

(7) RODENHISER, H. A.
1932. HETEROTHALLISM AND HYBRIDIZATION IN SPHACELOTHECA SORGHI AND S. CRUENTA. Jour. Agr. Research 45: 287–296, illus.

(8) TISDALE, W. H., MELCHERS, L. E., and CLEMMER, H. J.
1927. STRAINS OF KERNEL SMUTS OF SORGHUM, SPHACELOTHECA SORGHI AND S. CRUENTA. Jour. Agr. Research 34: 825–838, illus.

BELATED DEVELOPMENT OF KERNEL SMUT (SPHACELOTHECA SORGHI) IN APPARENTLY HEALTHY SORGHUM PLANTS[1]

By L. E. MELCHERS[2]

Head, Department of Botany, Kansas Agricultural Experiment Station

INTRODUCTION

One of the interesting features of infection experiments with kernel smut of sorghum, *Sphacelotheca sorghi* (Link) Clinton, is that the number of diseased plants seldom exceeds 50 percent even though heavily inoculated seed of highly susceptible varieties is planted under conditions favorable for the development of the disease. This peculiar characteristic has been noted repeatedly, and was indicated in a paper[3] concerning the resistance shown by different varieties of sorghums to *S. sorghi* over a period of 6 years in four regions of the United States. It has been observed that these relatively low percentages of kernel-smut infection in susceptible sorghums under field conditions are not greatly increased by the variable environment of the field. These results are unlike those obtained in other cereal diseases, such as bunt in wheat and the smuts in oats, where infections close to 100 percent may be obtained.

Experiments were conducted to determine whether this lack of smut development was due to an escape from infection as suggested by Martin,[4] or whether the disease merely failed to develop despite the presence of the smut organism in latent form in the host tissues. Studies were made of the response of different sorghum varieties (resistant and susceptible) to certain plant mutilations, and comparative tests were made with several physiologic forms of the kernel-smut fungus to learn whether all of them behave in a similar manner.

EXPERIMENTAL METHODS

The sorghum varietal plots which were used in studies on the physiologic forms of kernel smut[5] served also for the experimental material in the studies here reported. Self-pollinated seed of the several varieties of sorghum was heavily inoculated with chlamydospores of several physiologic forms of *Sphacelotheca sorghi* and planted at a time favorable for maximum infection.

The inoculum for these tests was prepared in two ways: (1) A composite mass of chlamydospores from several different forms of the organism was used; and (2) the different physiologic forms were kept separate so that their characteristics with respect to latent

[1] Received for publication Apr. 3, 1933; issued September 1933. Contribution no. 332, Department of Botany, Kansas State College of Agriculture and Applied Science.

[2] The writer gratefully acknowledges the assistance given by C. H. Ficke, C. O. Johnston, F. B. Bosley, and C. A. Wismer in these investigations.

[3] REED, G. M., and MELCHERS, L. E. SORGHUM SMUTS AND VARIETAL RESISTANCE IN SORGHUMS. U.S. Dept. Agr. Bul. 1284, 56 p., illus. 1925.

[4] MARTIN, J. H., and RATLIFFE, G. T. LOOSE KERNEL SMUT ON FETERITA. (Phytopathological note) Phytopathology 17: 338–339. 1927.

[5] MELCHERS, L. E., FICKE, C. H., and JOHNSTON, C. O. A STUDY OF THE PHYSIOLOGIC FORMS OF KERNEL SMUT (SPHACELOTHECA SORGHI) OF SORGHUM. Jour. Agr. Research 44: 1–11, illus. 1932.

smut invasion might be determined in both susceptible and resistant varieties of sorghum.

The details of inoculation, spacing, planting, etc., which were followed in these experiments are given in another publication.[6] Each row contained from 100 to 150 plants of the variety, selection, or hybrid. Approximately 105 varieties, selections, and hybrids of sorghum, *Sorghum vulgare* Pers., were used during the 4 years in which these studies were made.[7] Not all were planted each year, however, as table 1 shows.

It is a simple matter to determine whether a sorghum head is affected with kernel smut by the time the head emerges from the boot. If the head is normal, the stamens will soon extrude from the florets; but if kernel smut is present, the stamens do not appear, and a close examination will reveal the young smut galls or hypertrophied ovaries. It was at this stage that the apparently unsmutted plants were selected from each variety, selection, or hybrid for the experiments herein described.

Fifteen to twenty plants with unsmutted primary panicles were tagged in each row. These plants were mutilated in one of two ways during the course of the experiments. In 1929 and 1930 the normal primary heads were cut off at a point approximately 6 inches below the base of the panicle (fig. 1, A), and in 1931 and 1932 entire plants were also cut off at the level of the ground or a few inches above the ground (fig. 1, B).

Treatments of this type will cause the development of new shoots from axillary buds when the plant is merely beheaded and from sucker buds when the original stem is severed at the ground. The beheading treatment proved to be the better for this test, as heads were produced on the new growth in every instance, while the new tillers from sucker buds were seldom able to produce an inflorescence before frost. When the growing season was long enough for the new tillers to head out, the panicles in these tillers were smutted in several cases, indicating that there is mycelium of kernel smut within some plants of susceptible varieties which fail to produce smutted heads in the main tiller.

EXPERIMENTAL RESULTS

In Table 1 are shown (1) the percentages of kernel smut that occurred on the main heads of the varieties, selections, or hybrids as they grew naturally in the test plots, and (2) the percentages of kernel smut that developed on the same varieties, selections, and hybrids as a result of cutting back the apparently smut-free plants. The percentages of smut infection produced by cutting back were determined by dividing the number of heads that produced smut after this treatment by the number of mutilated plants. The percentages thus obtained should be a fair representation of the number of plants that are actually invaded by the kernel-smut fungus but that show no external indications of being diseased and so are usually counted as smut-free.

[6] Reed, G. M., and Melchers, L. E. Op. cit.

[7] The writer is indebetd to John H. Parker and A. F. Swanson, of the Kansas Agricultural Experiment Station and the Fort Hays Branch Experiment Station, respectively, for the seed of many of the varieties.

FIGURE 1.—A, Belated development of covered kernel smut of sorghum in axillary heads of Sagrain. The primary panicle was not smutted when it emerged from the boot. It was cut back as shown in the illustration. The plant, however, was infected with the smut organism as evidenced by the production of smutted axillary heads which developed later. B, Belated development of covered kernel smut of sorghum in secondary shoot or tiller of Kansas Orange × milo. The primary panicle was not smutted when it emerged from the boot. The entire plant was cut off near the ground. The new tiller produced a panicle that was affected by the kernel smut, *Sphacelotheca sorghi*.

TABLE 1.—*Percentage of kernel smut in mutilated sorghum plants as compared with the percentage on primary heads of nonmutilated plants; Manhattan, Kans., 1929–32*

Group, variety, or selection	Accession no.[b]	Percentage of kernel smut on—[a]									
		Primary heads, plants not cut back				Axillary heads of cut-back plants [c]				Heads of secondary tillers of cut-back plants	
		1929	1930	1931	1932	1929	1930	1931	1932	1931	1932
Sorgo:											
Atlas selection	K.B. 2505	21.4	3.3	----	----	0	0	----	----	----	----
Atlas selection no. 95	K.B. 2877	26.2	41.0	----	----	0	0	----	----	----	----
Atlas selection no. 100	K.B. 2878	26.7	----	----	----	0	----	----	----	----	----
Dwarf Sumac	K.B. 2576	32.4	32.6	----	----	7.5	13.3	----	----	----	----
Standard Sumac	K.B. 2902	27.4	27.9	----	----	0	0	----	----	----	----
Red Amber	K.B. 2504	16.2	2.0	----	----	0	0	----	----	----	----
Leoti Red	F.C.I. 6610	31.3	7.4	----	----	55.0	40.0	----	----	----	----
Kansas Orange	K.B. 2560	25.6	20.7	----	----	10.0	13.3	----	----	----	----
Japanese Honey Drip	K.B. 2876	29.6	26.0	----	----	0	6.7	----	----	----	----
Honey	K.B. 2874	32.6	----	----	----	0	----	----	----	----	----
Weskan	K.B. 2522	26.1	11.6	----	----	10	13.3	----	----	----	----
Freed	K.B. 2519	20.8	1.7	----	----	0	0	----	----	----	----
Dwarf Freed	K.B. 27107	32.4	0	----	----	0	0	----	----	----	----
Pink Freed (Tribune) no.	101–5(1926)	35.2	33.0	----	----	0	0	----	----	----	----
Kansas Orange	K.B. 3048	----	----	10.2	9.0	----	----	5	0	0	5
Red Amber × feterita:											
Selection	K.B. 2552	0	2.0	----	----	0	0	----	----	----	----
	K.B. 2513	0	0	----	----	0	0	----	----	----	----
	K.B. 2509	3.0	0	----	----	0	0	----	----	----	----
	K.B. 2562	0	0	0	0	0	0	0	0	0	0
	K.B. 2501	0	2.1	2.1	1	0	0	0	0	0	0
	K.B. 2567	----	1.6	----	----	----	0	----	----	----	----
	K.B. 2573	0	0	0	0	0	0	0	0	0	0
	K.B. 2570	21.5	6.0	0	5.5	25	13.3	0	0	0	0
Feterita:											
Selection	K.B. 2563	0	0	----	----	0	0	----	----	----	----
Hays selection	C.I. 182–1	0.4	0	----	----	0	0	----	----	----	----
Dwarf feterita no. 6	K.B. 2820	3.7	1.2	0	0	0	0	0	0	0	0
Red Leaf	K.B. 2543	2.2	2.8	0	0	0	0	0	0	0	0
Do	K.B. 2544	2.5	2.5	----	----	0	0	----	----	----	----
Feterita	S.P.I. 51989	0.5	2.1	0	0	0	0	0	0	0	0
Spur	K.B. 2540	0	0	0	0	0	0	0	0	0	0
Kafir:											
Reed	C.I. 628	3.8	20.8	----	----	10	0	----	----	----	----
Western Blackhull	K.B. 27102	21.0	29.4	----	----	0	0	----	----	----	----
Dawn	K.B. 2695	19.5	25.0	----	----	0	0	----	----	----	----
Do	K.B. 2538	20.6	20.0	----	----	0	0	----	----	----	----
Bishop	C.I. 814	----	----	0	0	----	----	0	0	0	0
Pink	K.B. 2546	26.7	19.7	----	----	0	0	----	----	----	----
Do	K.B. 2506	28.5	13.3	----	----	0	0	----	----	----	----
Do	F.C.I. 9091	35.6	18.8	----	----	5	13.3	----	----	----	----
Early Pink	K.B. 2824	27.2	19.7	----	----	5	20.0	----	----	----	----
Blackhull	K.B. 2535	16.2	13.9	----	----	5	26.7	----	----	----	----
Do	K.B. 3047	----	----	17.4	15.1	----	----	0	0	0	0
Red kafir	K.B. 2545	25.2	28.2	----	----	15	33.3	----	----	----	----
Club	C.I. 901	20.4	8.0	----	----	0	0	----	----	----	----
Modoc Pink Freed	K.B. 2831	20.1	30.0	----	----	0	0	----	----	----	----
Sunrise	K.B. 2523	21.1	----	----	----	0	----	----	----	----	----
Kafir × feterita:											
Hybrid	F.C.I. 8920	2.4	1.8	----	----	0	0	----	----	----	----
Pierce kaferita	K.B. 27101	8.4	1.2	----	----	0	0	----	----	----	----
Pierce kaferita selection	K.B. 2549	32.9	28.2	----	----	5.0	6.7	----	----	----	----
Do	K.B. 2547	4.1	0	0	0	0	6.7	5	0	0	0
Kaferita	C.I. 812	----	----	7.6	7.6	----	----	0	0	5	[d]
Hybrid	K.B. 2686	41.9	----	0	1.6	5.0	----	0	0	0	0
Premo	F.C.I. 8929	23.3	25.2	22.4	6.1	20.0	10.0	10	0	5	0

[a] The kernel smut used in 1929 consisted of physiologic forms 1 to 5, inclusive (MELCHERS, L. E., FICKE, C. H., and JOHNSTON, C. O. Op. cit.). Separate varietal plots were employed for each different smut used in 1929–32, inclusive. In 1930 the kernel smut consisted of a composite of forms 1 to 5, and the separate forms 1 to 5, inclusive. In 1931 only physiologic form 2 was used. In 1932 a composite of physiologic forms 1 to 5 and the separate forms 1, 2, and 3 were used.

[b] The letters C.I., F.C.I., S.P.I., and K.B. indicate accession numbers, respectively, of the Division of Cereal Crops and Diseases, Division of Forage Crops and Diseases, and Division of Foreign Plant Introduction, all of the Bureau of Plant Industry, U.S. Department of Agriculture, and of the Department of Botany of the Kansas Agricultural Experiment Station.

[c] The percentages derived from cutting back were determined by dividing the number of plants that produced smut after this treatment by the number of mutilated plants per row.

[d] Killed by frost.

TABLE 1.—*Percentage of kernel smut in mutilated sorghum plants as compared with the percentage on primary heads of nonmutilated plants; Manhattan, Kans., 1929–32*—Continued

Group, variety, or selection	Accession no.	Percentage of kernel smut on—									
		Primary heads, plants not cut back				Axillary heads of cut-back plants				Heads of secondary tillers of cut-back plants	
		1929	1930	1931	1932	1929	1930	1931	1932	1931	1932
Kafir × feterita—Continued											
Feterita × kafir	F.C.I. 6220			7.5	0			0	0	0	0
	F.C.I. 8951			5.5	8.3			0	10	5	(d)
	F.C.I. 8917	0.5	3.0	0	1.8	0	0	0	0	0	0
Kafir × milo hybrids:											
26-3-1-1	K.B. 2561	7.9	14.6	16.5	4.1	0	0	0	0	10	0
Dwarf Yellow milo × Pink kafir.	K.B. 2693	3.5	20.6	16.2	5.6	0	6.7	0	0	0	0
	K.B. 2694	4.3	9.5	6.7	5	5.0	13.3	5	5	0	0
	K.B. 2692	18.3	10.0			8.0	20.0				
	K.B. 3035			5.8	1.9			0	0	0	0
Kafir × milo 38-1-2-1	K.B. 2679	6.2	30.6			5.0	0				
Kafir × milo × Dwarf Yellow milo 31-79.	K.B. 3032			17.3	2.4			0	0	0	0
(Kafir × milo) × Dwarf Yellow milo No. 6.	K.B. 3033			0	1.6			0	0	0	0
Milo × kafir 8-2-6	K.B. 3034			1.7	13.0			(c)	0	0	0
Milo × feterita:											
Hybrid	F.C.I. 8926	0	0			0	0				
Milo and milo hybrids:											
Fargo Straightneck	C.I. 809	25.3	16.1	0	0	5.0	6.7	0	0	0	(d)
Dwarf Straightneck	K.B. 2844	5.3	2.2			0	0				
Open pollinated erect	K.B. 2845	6.5				0					
Dwarf Yellow	K.B. 2515	0	2.9	0	0	5.0	0	10	0	5	(d)
	C.I. 332	0	7.3	5.4	0	5.0	6.7	5	0	10	5
Standard White	C.I. 352	1.6	0			0	0				
Standard Yellow	C.I. 234	8.2	0			5.0	0				
Dwarf White	F.C.I. 8927	1.5	2.4			0	0				
Cream	K.B. 2569	2.5	4.5			0	0				
Double Dwarf	K.B. 3025			5.4	1.1			0	0	0	(d)
Sooner	K.B. 3027			21.7	0.9			0	0	10	0
Beaver	K.B. 3029			27.7	5.5			5	0	5	0
Early White	K.B. 3026			21.2	4.2			0	0	0	0
Early White No. 480 × Dwarf Yellow milo no. 332.	K.B. 3028			26.9	1.5			5	0	0	0
Wheatland	K.B. 3031			13.8	1.7			15	0	10	0
Kansas Orange sorgo × Dwarf Yellow milo:											
Selection	K.B. 2680	39.6	6.5			5.0	6.7				
	K.B. 2681	0	0			0	0				
	K.B. 2684	30.1				0					
Kansas Orange × milo	K.B. 3039			19.1	3.2			5	0	0	5
Hegari:											
Selection	K.B. 2518	0.2	0	0	0	0	0	0	0	0	0
	K.B. 2537	13.6	1.3	0	0	5.0	0	0	0	0	0
Broomcorn:											
Standard	C.I. 583	37.8	18.1			18.0	20.0				
Acme	C.I. 243	38.9	44.2	13.6	8.2	10.0	15.0	0	0	0	(d)
Kaoliang:											
Dwarf Shantung	C.I. 293	23.1	5.0			0	0				
Manchu Brown	C.I. 171	28.4	22.0	7.8	5.3	0	0	0	0	0	0
Miscellaneous:											
Wonder	K.B. 3010			5.1	6.7			15	0	10	0
Darso	K.B. 3003			8.1	3.4			5	0	5	0
	K.B. 2536	21.4	9.5			10.0	20.0				
White darso	K.B. 3002			3.4	9.4			0	0	0	0
Schrock	C.I. 616	9.2	5.7			10.0	0				
White durra	C.I. 81	31.1	19.8			5.0	6.7				
White Yolo	K.B. 2525	35.3	60.2	27.5	6.4	5.0	13.3	0	0	0	(d)
Shallu	C.I. 85	35.7	50.5	7.2	10.7	8.0	51.7	30	5	5	(d)
	K.B. 2879	38.6				13.0					
Sudan grass	K.B. 2981	6.4	7.6			0	0				
Manko maize	K.B. 3040			3.5	3.8			10	0	0	(d)
Oklahoma Johnny	K.B. 3044			32.5	6.8			10	0	0	0
Sagrain	K.B. 3004			17.5	7.0			0	5	0	(d)
Chiltex	F.C.I. 8917			24.2	16.9			0	0	15	0

d Killed by frost.

c 1 sucker.

It will be noted that such varieties as Leoti Red sorgo, Red Kafir, Dwarf Yellow milo, and shallu carry a high percentage of latent smut infection. Not all susceptible varieties, however, seem to carry large amounts and many carry very little. In 1929 out of a total of 176 heads of Leoti Red sorgo, 55 (31.3 percent) had primary head infection, and of the 20 normal heads cut back, 11 axillary heads (55 percent) developed smutted panicles. Had all of the 121 normal heads been cut back and the rate of smut infection on cut-back heads remained the same, there would have been 66.6 axillary heads and 55 primary heads, a total of 69.1 percent showing smutted panicles. On this basis it may be assumed that of the plants of Leoti Red sorgo actually invaded by the kernel-smut organism, only about half developed smutted panicles. The reaction of a resistant variety is not changed by cutting back, i.e., a resistant variety cannot be made susceptible. Resistance, therefore, is an inherited character, probably physiologic in nature.

The explanation for this reaction in sorghums is speculative, since the writer has not conducted histologic studies to demonstrate the presence of the smut fungus in the tissues of the host. From the studies that have been made it would appear that the following explanation may be the correct one.

The period during which infection by the kernel-smut fungus can occur is limited to 5 or 6 days immediately following the planting of the seeds. At this time, the infection hyphae evidently may gain entrance either to the meristematic tissue at the very apex of the growing point or to some of the embryonic cells a short distance back from the tip, where leaf and lateral bud primordia are beginning to differentiate. In the former case, short strands of hyphae would probably remain associated with the stem initials and the meristematic cells immediately behind them, and would also progress, through the agency of host cell division, to the cells in the basal portion of the meristematic region. As a consequence, not only the terminal inflorescence would be invaded and subsequently smutted, but there would also be a strong probability that the lateral buds, differentiating such a short distance behind would be similarly invaded. This might be tested by severing the inflorescences of diseased plants as soon as they emerge sufficiently from the boot to show that the smut mass is developing normally. If the supposition advanced above is correct, the disease should develop in the new panicles from lateral buds in every infected plant thus beheaded.

On the other hand, if the infection hyphae were to invade the meristematic region farther back where leaf and lateral stem differentiation are just taking place, and not in the apical cells, the division of the latter might result in the development of the growing point in advance of the infection hyphae and thus in its being able to grow away from the point of danger and produce a smut-free inflorescence. This would be particularly true if invasion of the meristematic tissues could be accomplished only by the division of cells containing mycelial fragments; otherwise, the hyphae would probably progress by intercellular invasion or direct penetration through cell walls, from the lateral cells of the apical meristem to the terminal cells. As Kolk [8]

[8] KOLK, L. A. RELATION OF HOST AND PATHOGEN IN THE OAT SMUT, USTILAGO AVENAE. Bul. Torrey Bot. Club 57: 443-507, illus. 1930.

has demonstrated, these two types of invasion occur in oat smut, and as a result the growing point is soon thoroughly infested with hyphae even though the point of infection may have been some distance removed. This is particularly significant in view of the fact that she had no difficulty in obtaining 100 percent smut development from inoculated seed. Likewise, in bunt, smutted plants may be obtained readily by seed inoculation, and it has been proved [9] that the mycelium may penetrate between the cells and from cell to cell.

The total number of varieties of sorghum infected with each form of kernal smut, after being cut back, and the percentage of kernel smut produced by cutting back are shown in table 2. The outstanding feature to be noted is that form 2, the milo kernel smut, produced diseased heads in the largest number of varieties and also usually produced the highest percentage of infection of plants within a variety.

TABLE 2.—*The number of varieties of sorghum and the percentage range of covered kernel smut infection produced by the various physiologic forms of Sphacelotheca sorghi in beheaded sorghum*

Year and physiologic form no.[a]	Number of varieties in the percentage class indicated									Total number varieties infected with each form
	0–4.9	5–9.9	10–14.9	15–19.9	20–24.9	25–29.9	55–59.9	80–84.9	90–94.9	
1929										
1		2	2		1					5
2		9	5	3	1		1			19
3		7	2							9
4		1	1		1					3
5		2	2	1		1				6
1930										
1		1							1	2
2		4	2		1			1		8
3			1			1				2
4		3								3
5		1	1							2

[a] Physiologic forms 1 to 5, inclusive, are the so-called kafir, milo, and 3 feterita forms of *S. sorghi*.

That form 2 should be more potent in this regard was not unexpected, for, as previous studies [10] had demonstrated, this form attacks not only all the varieties ordinarily susceptible to other forms but also the milos, some strains of hegari, and White Yolo, which are highly resistant to all other forms of kernel smuts to which they have been exposed in experiments at this station.

SUMMARY

Many sorghum plants among the susceptible varieties do not develop kernel smut in the primary heads even though the plants have the mycelium of *Sphacelotheca sorghi* within their tissues.

Cutting back infected plants that do not show kernel smut in the primary heads is often followed by the development of smut in the new growth of axillary shoots and in the shoots developed from sucker buds.

[9] WOOLMAN, H. M. INFECTION PHENOMENA AND HOST REACTIONS CAUSED BY TILLETIA TRITICI IN SUSCEPTIBLE AND NONSUSCEPTIBLE VARIETIES OF WHEAT. Phytopathology 20: 637–652, illus. 1930.

[10] MELCHERS, L. E., FICKE, C. H., and JOHNSTON, C. O. Op. cit.

Highly resistant or immune varieties of sorghum do not develop kernel smut in heads produced after the plants have been mutilated as described, i.e., resistant varieties evidently do not carry smut hyphae in their tissues. A variety that is really susceptible may appear resistant if judged only by the heads of original or main tillers.

The increase in kernel smut obtained by plant mutilation is directly proportional to the degree of susceptibility of the variety as expressed by primary head infection. Thus if a variety is very susceptible to kernel smut as shown by primary head infection, the percentage of kernel smut obtained by cutting back apparently smut-free plants will be proportionately large.

Five physiologic forms of *Sphacelotheca sorghi* were used as inoculum for sorghum seed in these studies. Form 2, the milo form, not only attacked a greater number of varieties, including the usually resistant milo, hegari, and White Yolo, but also caused a higher percentage of kernel smut within a variety than the four other forms.

The phenomena of infection and invasion of sorghum plants by the kernel-smut fungus have not been studied histologically, but possible explanation of these phenomena, based upon the results obtained in this experiment, is given.

U. S. GOVERNMENT PRINTING OFFICE: 1933